EARLY FOSSIL RECORD OF THE ASTERIDAE; REVISION, IDENTIFICATION, PHYLOGENETICS AND TIMING

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EARLY FOSSIL RECORD OF THE ASTERIDAE; REVISION, IDENTIFICATION, PHYLOGENETICS AND TIMING

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The Asteridae, a group characterized by fused corollas and iridoid compounds, comprises around 1/3-1/4 of all flowering plants, some 8000 species in 100-104 families, some of which, bear great economical importance (e.g. Solanaceae- tomato, potato, chili pepper, eggplant, tobacco; Rubiaceae-coffee; Theaceae-tea; Asteraceae- sunflower, lettuce, artichoke; Lamiaceae- oregano, thyme, sage, mint; Apiaceae- caraway, celery, dill; Ericaceae- blueberries, cranberries). Phylogenetic analyses have identified four main clades of asterids; Cornales, Ericales, Lamiids and Campanulids where the latter two correspond to Euasteridae.

A revision of 257 fossil taxa once assigned to the Asteridae showed that 172 (66%) could be considered accepted, based on three criteria: inclusion of the fossil in phylogenetic analysis, thorough discussion of key characters that place the fossil in a particular clade and list of key characters. The minimum age dating of the asterid phylogeny using these fossils revealed that the first two lineages, the Cornales and the Ericales were well established by the Late Cretaceous as evidenced by the fossils from the Turonian of Hydrangeaceae, Cornaceae, Ericaceae, Actinidiaceae and the newly described *Pentapetalum trifasciculandricus* related to the Theales. The other two lineages, Lamiids and Campanulids, were established shortly after, in the Santonian.

Although by traditional methods, *Pentapetalum* appear to be a member of the Theaceae s.s., cladistic analyses based on 61 morphological characters and 5 molecular markers (*rbcL*, *matK*, trnL-trnF, *matR* and ITS), placed it in the Pentaphylacaceae/Ternstroemiaceae.

Similar analyses, however, failed to solve the relationships of *Solanites brongniartii*, a presumed member of the Solanaceae from the Oligocene of France. The analysis using 23 morphological characters and 6 molecular markers (*rbcL*, *matK*, *ndhF*, *trnT-trnF*, *trnV* and *rps16*) offered six alternative placements for *S. brongniartii* but all of them within the Eusteridae. Other fossil species assigned to the genus *Solanites*, from the Eocene of North America, proved to have been misidentified as none of them fit the description for the genus. Three of them –*S. saportana*, *S. crassus* and *S. sarachaformis*– do not have enough characters to produce an accurate identification, but *S. pusillus* proved to be a member of the Rhamnaceae, a rosid family.

BIOGRAPHICAL SKETCH

Marcela Martínez Millán was born in Mexico City in October of 1976. The second of four children, she was raised by her great-aunts Eugenia and María del Carmen. Marcela attended *Institución Educativa Héroes de la Libertad* from elementary to high school, graduating in 1994. That year, she enrolled in the Biology major at *Facultad de Ciencias, Universidad Nacional Autónoma de México* (Faculty of Sciences, National Autonomous University of Mexico).

Although, always interested in paleontology –especially dinosaurs and other fossil reptiles–, the course "Paleobotany" taught by Dr. Sergio Cevallos Ferriz changed her views on fossil plants for life. So much that, during her 7th semester, Marcela joined Dr. Cevallos' Paleobotany Lab in the *Instituto de Geología, UNAM* (Institute of Geology, UNAM) to fulfill the social service requirement and to develop the research for her Bachelor's thesis.

In the spring semester of 1998, Marcela fulfilled all the credit requirements for her major and in the fall semester of the same year, she was hired by the Faculty of Sciences, UNAM to teach the laboratories of the course *Botánica III* (Botany III). After the 10-month-long strike at UNAM, she was finally able to defend her thesis titled *Biogeografía Histórica (Terciario y Cuaternario) de Anacardiaceae con base en caracteres anatómicos de la madera* (Historical Biogeography [Tertiary and Quaternary] of the Anacardiaceae based on wood anatomical characters) in July 10th of 2000, earning the degree of "Biologist" with *Mención honorífica*[*].

*_Mención honorífica_ is a high distinction granted for a thesis defense of exceptional quality voted unanimously by the exam jury provided other requirements (GPA) are also met.

That summer, she attended the VI International Organisation of Palaeobotany Conference in Qinhuangdao, China. There, she met Dr. Alejandra Gandolfo of Cornell University who awakened her interest in pursuing a PhD at .Cornell. However, that would have to wait for two more years as Marcela had already enrolled in the *Maestría en Ciencias Biológicas (Sistemática)* (Master in Biological Sciences [Systematics]) program at *Instituto de Geología*, *UNAM* with Dr. Sergio Cevallos as advisor.

Marcela's masters project, titled *Biogeografía Histórica (Terciario) de Anacardiaceae con base en arquitectura foliar* (Historical Biogeography [Tertiary] of the Anacardiaceae based on leaf architecture) was presented at the Botanical Society of America Conference, "Botany 2002" in Madison, WI where it won the Isabel Cookson Award for the best student oral presentation in Paleobotany. Marcela earned the degree of Master in Biological Sciences with *Mención honorífica* when she defended her thesis in July 17th 2003. Part of this work was published in the journal *Revista Mexicana de Biodiversidad* (76[2]: 137-190, 2005).

In the Fall of 2002, Marcela enrolled in the Field of Plant Biology PhD program at the L.H. Bailey Hortorium, Cornell University.

“Ay Babina, Babinilla…”

Porque tu amor y dedicación me alimentaron

Porque tu sacrificio y abnegación me forjaron

Porque gracias a ti, yo soy

Hija, esposa, estudiante y ahora, doctor;

Por todo eso; esta tesis es tuya

q.e.p.d 1918-2009

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Chapter 2* - Pentapetalum trifasciculandricus *gen. et sp. nov., a Thealean fossil flower from the Raritan Formation, New Jersey, USA. (Turonian, Late Cretaceous)— The authors thank J. Svitko for assistance with SEM, S. McNaull of Cornell Plantations for help locating plants in the living collection, and H. Ochoterena Booth for kindly sharing the matrix of morphological characters for the Theaceae. They also thank A. Gandolfo, L. Calvillo Canadell, and J. Salazar for fruitful discussion on the morphological characters and A. Gandolfo, M. Luckow, and two anonymous reviewers for comments on the manuscript. This research was supported by NSF grant DEB 0108369 to W.L.C. and K.C.N.

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CHAPTER 1

FOSSIL RECORD AND AGE OF THE ASTERIDAE*

INTRODUCTION

The Asteridae— The Asteridae is a group of flowering plants characterized by their fused corollas and iridoid compounds (Bremer et al., 2002). This group has been recognized by botanists since the eighteenth century, receiving names such as the Monopetalae, Gamopetalae or Sympetalae (Wagenitz, 1992) all of which allude to the characteristic connate corolla. In more recent times, classification systems based on morphology such as those of Cronquist (1981) and Takhtajan (1997), recognized relationships among several families displaying these characters and placed them in the similar subclass(es): Asteridae in the case of Cronquist (1981) and Asteridae, Lamiidae and Cornidae of Takhtajan (1997). With the advent of molecular systematics, the delimitation of the group has become clearer (Chase et al., 1993; Savolainen et al., 2000; Soltis et al., 2000; APG, 1998, 2003, 2009). Most of the taxa that Cronquist (1981) and Takhtajan (1997) placed in their Asteridae or separately in the Asteridae, Lamiidae and Cornidae are still accommodated in the current concept of Asteridae, but several other taxa traditionally placed in the Dillenidae and Rosidae have also been proven to be asterids (compare the three classification systems in Appendix A). This new, expanded and redefined Asteridae includes some 80,000 species in 102-106 families, that is, about 1/3-1/4 of all angiosperm species (APG, 1998, 2003, 2009; Bremer et al., 2002).

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The Asteridae as defined today is a remarkable group in many respects; for example, two of its families, Asteraceae (=Compositae, sunflower family) and Rubiaceae (coffee family) are among the most biodiverse plant families in terms of number of species. From an ecological and evolutionary point of view, Asteraceae (the sunflower family), Campanulaceae / Lobeliaceae (the bell-flower family) and Apocynaceae / Asclepiadaceae (the milkweed family) have some of the most specialized pollen presentation mechanisms in the plant kingdom. And from an economical perspective, important crops and other widely cultivated plants are asterids: tomato, potato, chili pepper, eggplant, tobacco (Solanaceae), tea (Theaceae), carrot, caraway, celery, dill (Apiaceae), oregano, thyme, sage, mint (Lamiaceae), sunflower, lettuce, artichoke (Asteraceae), coffee (Rubiaceae), blueberries and cranberries (Ericaceae).

Phylogenetic works focusing on all or parts of the Asteridae have substantially increased over the last few years (i.e. Hufford, 1992; Olmstead et al., 1992, 1993; Albach et al., 2001; Bremer et al., 2001, 2002; Lundberg and Bremer, 2003; Zhang et al., 2003; Chandler and Plunkett, 2004; Albach et al., 1998, 2005; Oxelman et al., 2005, Geuten et al., 2004; Schönenberger et al., 2005, etc) and have provided us with a more robust and better supported hypothesis of relationships among the asterid taxa. The most comprehensive study to date is that of Bremer et al. (2002) who focused on the whole of the Asteridae and included 132 genera in their analysis of six chloroplast markers (Figure 1.1). Their results, although consistent with previous studies that focused on all flowering plants (e.g. Chase et al., 1993; Savolainen et al., 2000; Soltis et al., 2000), are an important contribution towards resolving and understanding of the relationships among asterid lineages.

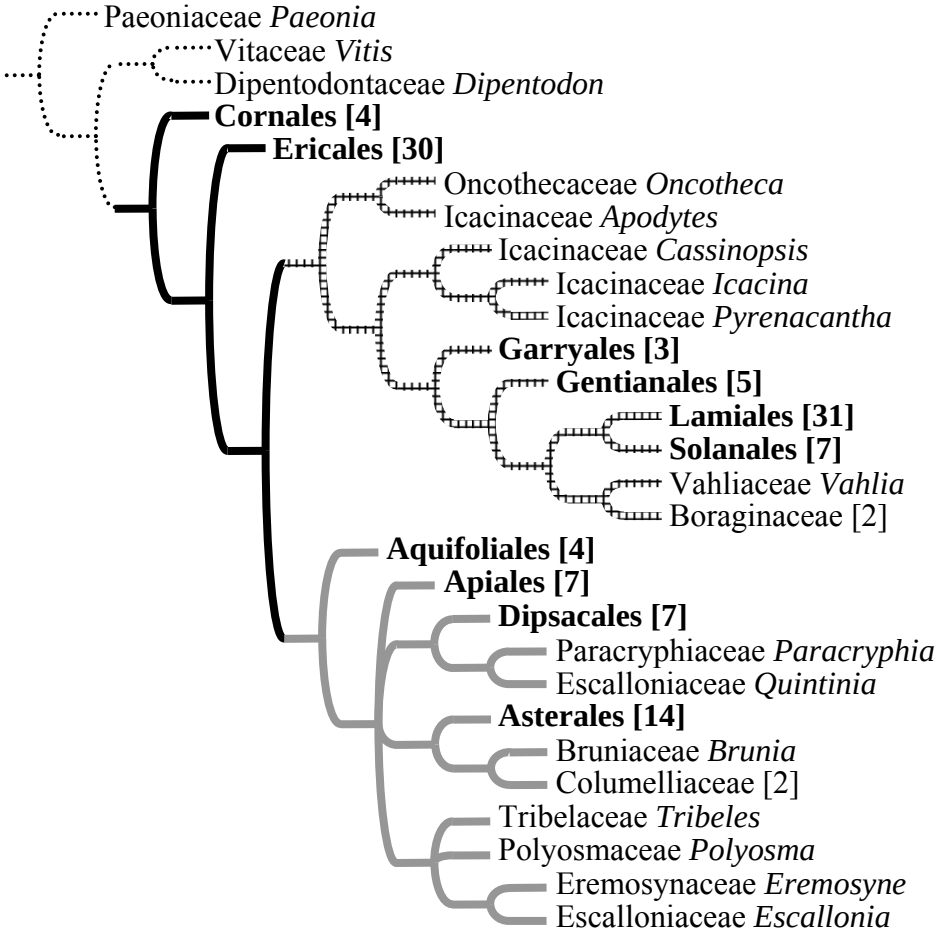


Figure 1.1. Phylogenetic relationships of Asteridae according to Bremer et al. (2002). Numbers in brackets indicate number of terminals used in the original analysis. Names in bold indicate Orders. Bold lines-Asterid clade, patterned lines-Lamiid clade (Euasterid I of Soltis et al. [2000] and APG [1998]), grey lines-Campanulid clade (Euasterid II of Soltis et al. [2000] and APG [1998]).

Bremer et al. (2002) identified four main clades (Figure 1.1): Cornales, Ericales, Lamiids and Campanulids. Cornales is sister to the rest of the Asteridae; Ericales is sister to the largest clade, the Euasteridae, formed by the Lamiids (formerly Euasterid I) and the Campanulids (formerly Euasterid II). The Euasteridae is where most of the diversity of the group is found (42.91% of all extant eudicot species [Magallón et al., 1999]).

Fossil Record of the Asteridae— Although the importance of the Asteridae has attracted attention in many areas of research and nearly 1/3 of all angiosperm species are asterids, their fossil record is not as extensive or even reflective of their extant diversity, especially in the large euasterid clade (*sensu* Soltis et al. [2000], APGII [2003] and Bremer et al. [2002]). Moreover, with the exception of selected families (e.g. Eucommiaceae by Call and Dilcher [1997], Symplocaceae by Kirchheimer [1949] and Mai and Martinetto [2006] or Cornaceae by Manchester [2002]), the relatively scarce fossil record of the group has never undergone specialized systematic revision or comprehensive treatment. For the most part, reports of fossils identified as asterids are scattered in paleofloral treatments, preliminary reports and short communications. As an additional problem, most of the reports are old –19th or early 20th Century– and poorly documented.

Estimating Ages of Divergence— Ever since the development of the concept of the molecular clock (Zuckerkandl and Pauling, 1962, 1965; Langley and Fitch, 1974) and of stochastic changes in the genome not subject to natural selection (i.e. neutral theory of molecular evolution [Kimura, 1983]), estimation of ages of divergence have no longer been the exclusive province of paleontology. Fossils alone do not pinpoint the place and time of origin of natural groups any more; instead they

are used in conjunction with methods that incorporate the current knowledge of molecular evolution and the vast reservoir of genomic data available. In recent years, with the increase in computational power, correlated new algorithms, and the better understanding of genome evolution and of phylogenetics, the interest in molecular dating has increased at an unprecedented rate (see Bromham and Penny [2003], Sanderson et al. [2004] and Welch and Bromham [2005] for reviews).

Today, it is widely accepted that genes do not necessarily evolve in a clock-like manner –i.e. according to a strict molecular clock *sensu* Langley and Fitch (1974)– and that different rates of evolution can be found in different genes, in different partitions and/or on different lineages (Sanderson, 2002). This has led to the development of techniques or methods that, coupled with those that estimate phylogenies themselves, give an estimate of timing in the divergence of lineages (clades) not based on a fixed molecular evolution rate. For example, Sanderson (1997) proposed NPRS (NonParametric Rate Smoothing), a method based on the assumption that evolutionary rates are not clock-like and can change from lineage to lineage (the estimation of that change is highly dependent on the rates of the descendant lineages). An improvement over this method that allows control of the level of smoothing through the introduction of a parameter is PL (Penalized Likelihood) also called Semiparametric Rate Smoothing (Sanderson, 2002). These methods and others have been widely applied to estimate ages of divergence of large clades across the entire tree of life (summarized in Hedges and Kumar, 2003; Magallón, 2004 and Welch and Bromham, 2005).

One feature that all these methods have in common is their need for at least one (but often more) calibration or constraint point(s) which will help determine the

rate(s) at which the genomic sequences change. In a very simplified way, the number of base differences / time = rate of molecular substitution. Since the fossil record is the main source of calibration point(s) for these analyses, it is of the utmost importance that the fossils used are reliable, both in terms of taxonomic identity and in terms of age. Unfortunately misidentifications of taxa are common in the fossil record, especially in the case of angiosperms. As Collinson et al. (1993) remarked, "These problems have been exacerbated in the past by a common tendency to include fossils in modern taxa based on superficial similarity rather than in-depth analysis. Although the latter is now the rule rather than the exception, many older determinations have not yet been revised."

Other methods that do not use molecular sequences such as minimum-age-dating still depend on a reliable fossil record. Minimum-age-dating assigns ages to the different nodes in the phylogeny by choosing the oldest date among the daughter nodes descended from the node in question (Crepet et al., 2004). Progressing this way along the tree, it is possible to assign objective minimum ages to each node in the phylogeny. This method, although free from the pitfalls that plague rate estimation, is very susceptible to errors due to misidentifications and taxonomic misplacements of fossils. Due to its influence and central role in both kinds of methods, molecular-based and fossil-only-based, it is highly desirable that the fossil record be revised and that the reliability of fossils used to assign ages to phylogenies be assessed.

Estimated Age for the Asterids— One of the earliest attempts to date the angiosperm phylogenetic tree by incorporating fossil data into the angiosperm phylogeny was that of Magallón et al. (1999) who assigned dates to the nodes of the Eudicot clade of the Chase et al. (1993) cladogram by referencing the fossil record.

While they did not explicitly date the asterid clade in that study, its "older" order, the Ericales was assigned a date of 89.5 my (Table 1.1). More recently, Crepet et al. (2004) assigned minimum ages to the early lineages of the angiosperm phylogeny of Soltis et al. (2000) using the fossil record. Although that work deals with the earliest nodes on the angiosperm phylogeny and not with the more derived groups, the minimum age for the Asterid clade (90 my; Table 1.1) is similar to that reported by Magallón et al. (1999). Age estimates of the angiosperms as a whole, based on molecular clock techniques (Wikström et al., 2001) give an older estimate for the origin of the Asterid clade (112-122 my, Table 1.1) while studies focusing on the Asteridae alone (Bremer et al., 2004) give an even older date, somewhere before 128 million years ago (Table 1.1). The results of these studies imply a gap of at least 22 million years for which, if accurate, the early asterids left no identifiable fossil record. Only through careful revision and critical study of the fossils upon which these age estimates are based would we be able to assess if this discrepancy is real or is an artifact of the methods. Did the asterids not leave a recognizable fossil record for 22 million years? Or, is the proposed 128 million years an inaccurate estimate?

The accurate dating of correctly identified fossils is critical in any age estimation, based either on fossil record alone or in molecular dating techniques with fossil calibration points. Even the best method for molecular dating will generate meaningless results if the original calibration point(s) on which the whole analysis is/are based, is not reliable (Crane et al., 2004; Graur and Martin, 2004; Benton and Donoghue, 2007). The two problem areas that need to be critically evaluated before a fossil taxon can be accepted as a reliable calibration point are: [1] the certainty of its taxonomic placement and [2] the correctness of the age assignment of the sediments in which the fossil was found, which implies an understanding and a correct

interpretation of the geological time scale. This work is a step towards achieving a better understanding of the early Asterid fossil record; by evaluating the reliability of those fossils that could potentially represent the earliest members of asterid families, by producing a time scale for Asterid diversification based on the reliable fossils identified and applying minimum-age-dating, and by comparing this fossil-based time scale to molecular-based age estimates.

Table 1.1. Estimated times of divergence of relevant angiosperm groups based on fossil estimates and molecular dating, ages are given in millions of years before present (MYBP).

Clade	Magallón et al., 1999	Wikström et al., 2001	Bremer et al., 2004	Crepet et al., 2004
Estimate	fossil	molecular	molecular	fossil
Angiosperms	---	158-179	---	113
Eudicots	---	131-147	---	100
Asterids	---	112-122	---	90
Cornales	69.5	106-114	128	---
Ericales	89.5	106-114	127	90
Euasterids	---	107-117	127	---
Campanulids	---	102-112	123	---
Aquifoliales	69.5	99-107	121	---
Apiales	69.5	85-90	113	---
Dipsacales	53.2	85-90	111	---
Asterales	29.3	101-94	112	---
Lamiids	---	102-112	123	---
Garryales	45.9	100-107	114	---
Gentianales	53.2	83-89	108	---
Solanales	53.2	82-86	106	---
Lamiales	37	71-74	106	---

MATERIALS AND METHODS

Literature review— The evaluation of the fossil record started with a literature search of the fossils that have been published as having affinities with groups that today constitute the Asteridae (*sensu* Bremer et al. [2002]). The search focused on the family level, that is, on the oldest fossils ever reported for each one of the 100-104 families that constitute the group. However, fossils unassigned to family but to higher taxonomic levels were also considered. In the assembling of this list, original descriptions and monographs were preferred.

Evaluation of fossils— Each one of the fossils was evaluated with respect to the reliability of its identification by reviewing their protologues or monographs. Eight criteria were taken into consideration for each fossil, each one evaluated as provided/not provided by the authors. In order of decreasing reliability the criteria are: [1] inclusion of the fossil in a phylogenetic analysis, [2] discussion of key characters that place the fossil in a group, [3] list of key characters that place the fossil in the group, [4] full taxonomic description and diagnosis of the fossil, [5] photographs of the specimens, [6] drawings, diagrams or reconstructions of the fossils, [7] specimen information; housing institution, collection number, holotype designation, [8] collection information; locality, formation, age.

Once the list was compiled, it was subject to a filter designed to identify the reliable and well supported records by focusing on those fossils that fulfilled the first three criteria. These fossils were accepted as representing reliable records. The remainder of the list was subject to a second filter for which the criterion was the existence of a reliable older fossil belonging to the same family. That is, once a fossil

was accepted as member of a family, any younger fossils assigned to that family were excluded from further analysis because they could no longer be considered evidence of the first appearance of that family. The fossils that were not removed by either filter are not only ambiguous and in need of revision but also potentially the earliest evidence for a family/order of Asteridae, that is, the putative oldest evidence of a lineage.

Age determinations— The age assigned to the fossils follows the most recent accepted date for the sediments in which they are found, and not the age that was assigned to them when they were first described. This is important to consider, especially with regard to older reports in which boundaries for time periods were differently defined. For the purpose of assigning numerical dates to time periods, the upper bound (end) of that period as defined in the International Geologic Time Scale (Gradstein et al., 2004) was used.

Minimum age dating— The fossils accepted as reliable after applying criteria mentioned above were incorporated as minimum age indicators in a phylogeny of the Asteridae following the method of Crepet et al. (2004). The asterid cladogram used is based on the results of Bremer et al. (2002) modified by the substitution of particular clades that are now available and that represent more comprehensive and resolved cladograms for those particular groups: Zhang et al. (2003) for Dipsacales, Chandler and Plunkett (2004) for Apiales, Lundberg and Bremer (2003) for Asterales, Oxelman et al. (2005) for parts of Lamiales and Schönenberger et al. (2005) for Ericales.

RESULTS

Fossil Record of the Asteridae— A total of 261 fossils once described as asterids were identified (Table 1.2). This list should not be considered exhaustive since many younger reports were not included in instances where older, reliable reports had been already listed. Also, reproductive structures were favored over vegetative structures because it is in the reproductive structures that synapomorphies and diagnostic characters of the groups are more likely to be found. Therefore, this list should not be considered a fair representation of the status of the uncritically assessed asterid fossil record; however, it does provide a more accurate assessment of asterid history and also represents a coarse approximation of the abundance of fossil reports for the different clades. From this listing, it can be seen that, although some families (e.g. Fouqueriaceae, Loasaceae) have no reported fossil record, in the end, all orders are represented in the fossil record.

The order of asterids with the best fossil record is the Ericales (Table 1.2), with 80 reports; however, this apparent abundance of ericalean taxa is misleading since a good portion of these records is based on reports of the genus *Symplocos*, monographed in 1949 by Kirchheimer. If the taxa described in that work were removed, only 48 records would remain, leaving the Ericales as the most frequently reported order of asterids, but with a more modest advantage.

Of the two clades of the Euasteridae, the Lamiids (Euasteridae I) present a more abundant fossil record than its counterpart, the Campanulids (Table 1.2). However, it is noticeable that despite the biodiversity these two groups display today,

their fossil record combined is barely larger than the combined fossil record of the two early diverging orders, the Cornales and the Ericales.

Table 1.2. Summary of the fossil record of Asteridae by orders. Numbers indicate the number of fossil occurrences found during the literature review before evaluating each record. "reproductive" includes macrofossil remains of flowers, fruits and seeds, "vegetative" mostly includes leaves and wood. Six fossils are represented twice since they are known from organically connected reproductive and vegetative remains. "Unplaced families" include the clades Escalloniaceae-Paracryphiaceae (Paracryphiales of APG [2009]), Icacinaceae-Oncothecaceae and Boraginaceae-Vahliaceae (see Figure 1.1).

Order	fossils	reproductive	vegetative	pollen
Cornales	21	17	4	2
Ericales	81	49	24	10
Campanulids	*56*	*40*	*6*	*10*
Aquifoliales	5	3	0	2
Apiales	18	16	1	1
Dipsacales	8	5	2	1
Asterales	24	15	3	6
Lamiids	*103*	*58*	*30*	*16*
Garryales	11	7	2	2
Gentianales	24	9	7	8
Solanales	14	9	2	3
Lamiales	24	16	8	2
Unplaced families	31	18	12	1
TOTAL	*261*	*164*	*65*	*38*

Cornales— The Cornales is a well supported and well studied group, however, different authors treat the families Cornaceae, Nyssaceae and Mastixiaceae differently. Under some schemes, the families are treated as one broadly defined Cornaceae, while other authors prefer to treat them as separate, although closely related, families (see Xiang et al. [2002] and Fan and Xiang [2003]). In this work, they will be referred to as different families, as that provides more information as to the inferred relationships of the fossils. The oldest reliable fossils for this clade are *Hironoia fusiformis*, a "cornalean" fruit from the Coniacian-Santonian of Japan and *Tylerianthus crossmanensis*, a fossil flower from the Turonian of New Jersey (Table 1.3, Figure 1.2). Although initially *Tylerianthus* was described as having affinities with the Hydrangeaceae or the Saxifragaceae, the authors indicate that cladistic analyses placed it as sister to Hydrangeaceae. Later, Crepet et al. (2004) confirmed the placement of *Tylerianthus* in that family. This fossil places the Order in at least the Turonian (Figure 1.2).

Table 1.3. Early fossil record of the Cornales. Acc = accepted.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Hydrangeaceae					
Tylerianthus crossmanensis Gandolfo, Nixon et Crepet 1998	flower	Turonian	Raritan, NJ, USA	Gandolfo et al., 1998	yes
Cornaceae					
Cornus clarnensis Manchester 1994	endo_carp	Middle Eocene	Clarno, OR, USA	Manchester, 1994	yes
Mastixioxylon symplocoides Meijer 2000	wood	Middle-Late Santonian	Aachen, La Calamine, NE Belgium	Meijer, 2000	yes
Cornaceae/Nyssaceae					
Nyssoxylon sp.	wood	Middle-Late Santonian	Aachen, La Calamine, NE Belgium	Meijer, 2000	yes

Table 1.3. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Nyssaceae					
Davidia antiqua (Newberry) Manchester 2002	leaf/ fruit	Early Paleocene	Bureya, SE Russia	Manchester, 2002	yes
Davidia antiqua (Newberry) Manchester 2002	leaf/ fruit	Paleocene	Fort Union Gr, ND, MT, WY, USA	Manchester, 2002	yes
Nyssa	pollen	Middle Oligocene	San Sebastián Puerto Rico	Graham and Jarzen, 1969	no
Nyssa sp.	endo_ carp	Early Ypresian, Early Eocene	Nanjemoy, VA, USA	Tiffney, 1999	yes
Tricolporopollenites kruschii Potonié 1934	pollen	Paleocene	Wilcow flora, TX, USA	Elsik, 1968	no
Nyssaceae/Mastixiaceae					
Hironoia fusiformis Takahashi, Crane et Manchester 2002	fruit	Early Coniacian-Early Santonian	Ashizawa Fm, NE Honshu Japan	Takahashi et al., 2002	yes
Mastixiaceae					
Beckettia sp.	fruit	Early Ypresian, Early Eocene	Nanjemoy, VA, USA	Tiffney, 1999	yes
cf. *Mastixia*	endo_ carp	Early Paleocene-Earliest Eocene	Fort Union, WY, USA	Tiffney and Haggard, 1996	yes
cf. *Mastixia*	fruit	Late Early Eocene-Early Middle Eocene	Sepulcher, MT-WY, USA	Tiffney and Haggard, 1996	yes
Diplopanax eydei Stockey, LePage et Pigg 1998	fruit	Middle Eocene	Princeton Chert, BC, Canada	Stockey et al., 1998	yes
Langtonia bisulcata Reid et Chandler 1933	endo_ carp	Early Eocene	London Clay, England	Reid and Chandler, 1933	yes
Langtonia bisulcata Reid et Chandler 1933	endo_ carp	Late Early-Middle Paleocene	Fort Union, WY, USA	Tiffney and Haggard, 1996	yes
Langtonia bisulcata Reid et Chandler 1933	endo_ carp	Early Paleocene-Earliest Eocene	Fort Union, WY, USA	Tiffney and Haggard, 1996	yes
Langtonia bisulcata Reid et Chandler 1933	endo_ carp	Middle Eocene	Clarno, OR, USA	Manchester, 1994	yes
Mastixia eydei Tiffney et Haggard 1996	endo_ carp	Late Eocene	Auriferous Gravels, CA, USA	Tiffney and Haggard, 1996	yes
Mastixia oregonense (Scott) Tiffney et Haggard 1996	endo_ carp	Middle Eocene	Clarno, OR, USA	Tiffney and Haggard, 1996	yes
Mastixicarpum occidentale Manchester 1994	endo_ carp	Middle Eocene	Clarno, OR, USA	Tiffney and Haggard, 1996	yes

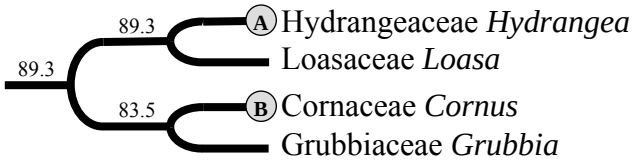


Figure 1.2. Minimum age dating of the Cornales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Bremer et al. (2002). A- *Tylerianthus crossmanensis*, Turonian (89.3 mya). B- *Hironoia fusiformis*, Santonian (83.5 mya).

Ericales— The ericalean clade in the both the Bremer et al. (2002) and Schönenberger et al. (2005) analyses is composed of two sister clades, one includes Marcgraviaceae, Balsaminaceae, *Tetramerista* and *Pelliciera*, the "balsaminoid" clade, and the other one includes the rest of the Ericales. From the balsaminoid clade, pollen grains representing Pellicieraceae (=Tetrameristaceae in the Schönenberger et al. [2005] analysis) and Marcgraviaceae have been reported from several localities around the neotropics (Table 1.4). However, none of these reports have provided a detailed account of the characters that identify these fossils as *Pelliciera*, *Marcgravia* or *Norantea*. For this reason these reports are not accepted in the present treatment. It is interesting to notice, however, that the clade has only been reported in the palynological fossil record, no macrofossils have been assigned to this group.

The second clade includes families with no known fossil record such as Fouqueriaceae and Sarraceniaceae, and families with relatively extensive fossil records, like Ebenaceae and Symplocaceae. This group includes many arborescent members whose fossil record is mostly wood (e.g. Ebenaceae, Theaceae, Lecythidaceae).

Table 1.4. Early fossil record of the Ericales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Marcgraviaceae					
Marcgravia sp	pollen	Middle Oligocene	San Sebastián Puerto Rico	Graham and Jarzen, 1969	no
Norantea sp	pollen	Middle Oligocene	San Sebastián Puerto Rico	Graham and Jarzen, 1969	no
Tetrameristaceae ("Pellicieraceae")					
"*Pelliciera*"-like	pollen	Oligocene-Miocene	Simojovel, Chis, Mexico	Lagenheim et al., 1967	no
Pelliciera	pollen	Early Middle Eocene	Chapelton, Jamaica	Graham, 1977	no
Pelliciera	pollen	Eocene	Gatuncillo, Panamá	Graham, 1977	no
Pelliciera	pollen	Oligocene-Miocene	La Boca, Panamá	Graham, 1977	no
Pelliciera	pollen	Oligocene-Miocene	La Quinta, Chis, Mexico	Graham, 1999	no
Pelliciera	pollen	Middle Oligocene	Sn Sebastián, Puerto Rico	Graham and Jarzen, 1969	no
Psilatricolporites crassus van der Hammen et Wigmstra 1964	pollen	Tertiary	Guiana Basin, Guianas	Graham, 1977	no
Lecythidaceae					
Barringtonioxylon arcotense Awasthi 1969	wood	Tertiary	Cuddalore Series, India	Awasthi, 1969a	yes
Barringtonioxylon eopterocarpum Prakash et Dayal 1964	wood	Early Tertiary (Eocene?)	Deccan Intertrappean Beds, India	Prakash and Dayal, 1964	yes
Careyoxylon pondi_ cherriense Awasthi 1969	wood	Tertiary	Cuddalore Series, India	Awasthi, 1969a	yes
Sapotaceae					
Chrysophyllum tertiarum Mehrotra 2000	leaf	Late Paleocene	Nangwalbibra India	Mehrotra, 2000	yes
Ebenaceae					
Austrodiospyros cryptostoma Basinger and Christophel 1985	flower/ leaf	Late Eocene	Anglesea, Victoria, Australia	Basinger and Christophel, 1985	yes
Diospyros palaeoebenum Prasad 1994	leaf	Middle Miocene-Pliocene	Siwalik, Nepal	Prasad and Pradhan, 1998	yes
Ebenoxylon arcotense Awasthi 1969	wood	Tertiary	Cuddalore Series, India	Awasthi, 1969b	yes
Ebenoxylon kalagarhensis Prasad 1988	wood	Middle Miocene	Siwalik, India	Prasad, 1988	no
Ebenoxylon kartikcherrense Prakash et Tripathi 1969	wood	Late Miocene	Kartikcherra, India	Prakash and Tripathi, 1969	yes
Ebenoxylon miocenicum Prakash 1978	wood	Middle Miocene	Siwalik, India	Prasad, 1993	yes

Table 1.4. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Ebenoxylon palaeo_ candoleana Prasad 1993	wood	Middle Miocene	Siwalik, India	Prasad, 1993	yes
Ebenoxylon siwalicus Prakash 1981	wood	Middle Miocene	Siwalik, India	Prasad, 1993	yes
Myrsinaceae					
Ardisia palaeosimplicifolia Prasad 1994	leaf	Middle Miocene-Pliocene	Siwalik, Nepal	Prasad and Pradhan, 1998	yes
"Myrsinaceae"	leaf	Early Miocene	Foulden Hills, New Zealand	Pole, 1996	yes
Polemoniaceae					
Gilisenium hueberi Lott, Manchester et Dilcher 1998	plant	Middle Eocene	Green River, UT, USA	Lott et al., 1998	yes
Theaceae					
Andrewsiocarpon henryense Grote et Dilcher 1989	seed/ fruit	Middle Eocene	Claiborne Fm, KY, TN, USA	Grote and Dilcher, 1989	yes
Gordonia lamkinensis Grote et Dilcher 1992	fruit	Middle Eocene	Claiborne Fm, KY, USA	Grote and Dilcher, 1992	yes
Gordonia warmanensis Grote et Dilcher 1992	fruit	Middle Eocene	Claiborne Fm, TN, USA	Grote and Dilcher, 1992	yes
Gordoniopsis polysperma Grote et Dilcher 1992	fruit	Middle Eocene	Claiborne Fm, TN, USA	Grote and Dilcher, 1992	yes
Pentaphylacaceae ("Ternstroemiaceae")					
Eurya crassitesta Knobloch 1975	seed	Maastrichtian-Paleocene	Eisleben, Germany	Mai, 1987	yes
Eurya microstigmosa Mai 1987	seed	Early Paleocene	Gunna, Germany	Mai, 1987	yes
Eurya stigmosa (Ludwig) Mai 1987	seed	Paleocene	Eisleben, Germany	Mai, 1987	yes
Pentaphylacaceae ("Sladeniaceae")					
Sladenioxylon africanum Giraud, Bussert et Schrank 1992	wood	Albian-Cenomanian	Wadi Awatib, Sudan	Giraud et al., 1992	yes
Pentaphylacaceae ("Pentaphylacaceae")					
Pentapetalum trifasciculan_ dricus Martínez-Millán, Crepet et Nixon, 2009	flower	Turonian	Raritan, New Jersey	Martínez-Millán et al., 2009	yes
Actinidiaceae/Theaceae					
Paradinandra suecica Schönenberger et Friis 2001	flower	Late Santonian-Early Campanian	Asen, Scania, N Sweden	Schönenberger and Friis, 2001	yes
Actinidiaceae					
Actinidia argutaeformis Dorofeev 1963	seed	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_ doniowa, 1979	yes

Table 1.4. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Actinidia faveolata Reid 1915	seed	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_ doniowa, 1979	yes
Actinidia oregonensis Manchester 1994	seed	Middle Eocene	Clarno, OR, USA	Manchester, 1994	yes
Parasaurauia allonensis Keller, Herendeen et Crane 1996	flower	Early Campanian	Gaillard Fm, Buffalo Creek GA, USA	Keller et al., 1996	yes
Saurauia antiqua Knobloch et Mai 1986	seed	Senonian-Santonian	Klikov-Schichtenfol_ ge, Germany	Knobloch and Mai, 1986	yes
Ericaceae					
"Ericaceae"	pollen	Oligocene-Miocene	La Quinta, Chis, Mexico	Graham, 1999	no
Paleoenkianthus sayrevillensis Nixon et Crepet 1993	flower	Turonian	Raritan, New Jersey	Nixon and Crepet, 1993	yes
Diapensiaceae					
Actinocalyx bohrii Friis 1985	flower	Late Santonian-Early Campanian	Asen, Scania, S Sweden	Friis, 1985	yes
Styracaceae					
Rehderodendron stonei (Reid et Chandler) Mai 1970	fruit	Eocene	Sabals d' Anjou, France	Vaudois-Mieja, 1983	yes
Styrax hradekense Schweigert 1992	leaf	Oligocene	Hessenreuth, Germany	Schweigert, 1992	yes
Symplocaceae					
Durania ehrenbergii Kirchheimer 1949	endo_ carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	yes
Palliopora symplocoides Kirchheimer 1949	endo_ carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	yes
Sphenoteca gigantea Kirchheimer 1949	endo_ carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	yes
Sphenoteca incurva Kirchheimer 1949	endo_ carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	yes
Symplocos arecaeformis (Schlotheim) Kirchheimer 1949	endo_ carp	Middle-Late Oligocene	Rheinland, Germany & Poland	Kirchheimer, 1949	yes
Symplocos braunii Kirchheimer 1949	endo_ carp	Late Miocene	Hessen, Germany	Kirchheimer, 1949	yes
Symplocos bureauana Saporta 1868	leaf	Early Eocene	Marne, France	Kirchheimer, 1949	no
Symplocos casparyi Ludwig 1857	endo_ carp	Early Miocene-Early Pliocene	Hessen, Germany	Kirchheimer, 1949	yes

Table 1.4. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Symplocos cf. *crataegoides* Buchanan-Hamilton 1937	endo_carp	Early Pliocene	Hessen, Germany	Kirchheimer, 1949	no
Symplocos commutatifolia Berry 1938	leaf	Eocene	Rio Pichilefu, Argentina	Kirchheimer, 1949	no
Symplocos detrita Velenovsky 1882	leaf	Early Miocene	Vrsovice, Czech Rep.	Kirchheimer, 1949	no
Symplocos elongata Ludwig 1857	endo_carp	Early Pliocene	Hessen, Germany	Kirchheimer, 1949	no
Symplocos globosa Ludwig 1857	endo_carp	Early Pliocene	Hessen, Germany	Kirchheimer, 1949	no
Symplocos gothani Kirchheimer 1949	endo_carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	yes
Symplocos grimsleyi Tiffney 1999	endo_carp	Early Ypresian, Early Eocene	Nanjemoy, VA, USA	Tiffney, 1999	yes
Symplocos headonensis Chandler 1926	fruit	Late Eocene	Hampshire, UK	Kirchheimer, 1949	no
Symplocos kirstei Kirchheimer 1939	endo_carp	Early-Middle Oligocene	Thüringen, Germany	Kirchheimer, 1949	no
Symplocos laurifolia Hofmann 1926	leaf	Miocene	Kathrein, Austria	Kirchheimer, 1949	no
Symplocos lignitarum (Quenstedt) Kirchheimer 1949	endo_carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	yes
Symplocos ludwigii Kirchheimer 1949	endo_carp	Early Pliocene	Hessen, Germany	Kirchheimer, 1949	yes
Symplocos microcarpa Reid 1920	endo_carp	Early Pliocene	Pont-de-Gail, France	Kirchheimer, 1949	no
Symplocos minutula (Sternberg) Kirchheimer 1949	endo_carp	Early Oligocene-Late Miocene	Rheinland, Germany, Switzerland, Austria, France, Czech Rep, Poland	Kirchheimer, 1949	yes
Symplocos n. sp. Reid 1923	endo_carp	Early Pliocene	Pont-de-Gail, France	Kirchheimer, 1949	no
Symplocos oleaceae Ludwig 1858	endo_carp	Late Miocene	Hessen, Germany	Kirchheimer, 1949	yes
Symplocos oregona Chaney et Sanborn 1933	leaf	Late Eocene	Goshen, Oregon, USA	Kirchheimer, 1949	no
Symplocos poppeana Kirchheimer 1940	endo_carp	Middle-Late Oligocene	Lausitz, Germany	Kirchheimer, 1949	no
Symplocos pseudogregaria Kirchheimer 1949	endo_carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	no

Table 1.4. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Symplocos quadrilocularis Reid et Chandler 1933	fruit	Early Eocene	Minster, Kent, UK	Kirchheimer, 1949	no
Symplocos radobojana Unger 1866	fruit	Late Oligocene-Early Miocene	Radoboj, Yugoslavia, Czech Rep	Kirchheimer, 1949	no
Symplocos salzhausenensis (Ludwig) Kirchheimer 1949	endo_carp	Late Miocene	Hessen, Germany	Kirchheimer, 1949	no
Symplocos schereri Kirchheimer 1935	endo_carp	Middle-Late Oligocene	Rheinland, Germany	Kirchheimer, 1949	no
Symplocos smithii Florin 1920	leaf	Late Pliocene	Amakusa, Japan	Kirchheimer, 1949	no
Symplocos sp. Kirchheimer 1949	endo_carp	Late Eocene-Early Pliocene	Hessen, Germany, England, Netherlands	Kirchheimer, 1949	no
Symplocos subspicata Friedrich 1883	leaf	Eocene	Eisleben, Germany	Kirchheimer, 1949	yes
Symplocos trilocularis Reid et Chandler 1933	fruit	Early Eocene	Minster, Kent, UK	Kirchheimer, 1949	no
Symplocos urceolata Reid 1920	fruit	Early Pliocene	Pont-de-Gail, France	Kirchheimer, 1949	no
Symplocos wiesaensis Kirchheimer 1949	endo_carp	Middle-Late Oligocene	Lausitz, Germany	Kirchheimer, 1949	no

The most remarkable of ericalean fossils are the fusainized flowers found in Cretaceous sediments in different localities of Eastern North America (New Jersey and Georgia), Europe (Sweden) and Japan (Crepet, 1996; Crane and Herendeen, 1996; Herendeen et al., 1999; Takahashi et al., 1999; Friis et al., 2006). The preliminary surveys of these floras indicate that ericalean flowers are abundant and diverse in these localities. Unfortunately many of them have not been formally described and the ones that have been described frequently show an array of characters not found in modern genera and sometimes not completely conforming to the families to which they are believed to be related. The fossil record also indicates that many modern families were well established by the Eocene (Figure 1.3) as evidenced by very complete fossils that include both, vegetative and reproductive structures (i.e. Christophel and Basinger 1982; Basinger and Christophel, 1985; Lott et al., 1998).

As of today, the oldest representatives of Ericales are *Paleoenkianthus sayrevillensis* (Nixon and Crepet, 1993) and *Pentapetalum trifasciculandricus* (Martínez-Millán et al., 2009), both from the Turonian of New Jersey (Table 1.4). These two fossils have been associated to clades that in the most recent phylogenetic hypothesis are not too closely related (Figure 1.3), the Ericaceae and a part of the Theaceae *s.l.* that Schönenberger et al. (2005) call the Pentaphylacaceae and Bremer et al. (2002), the Ternstroemiaceae.

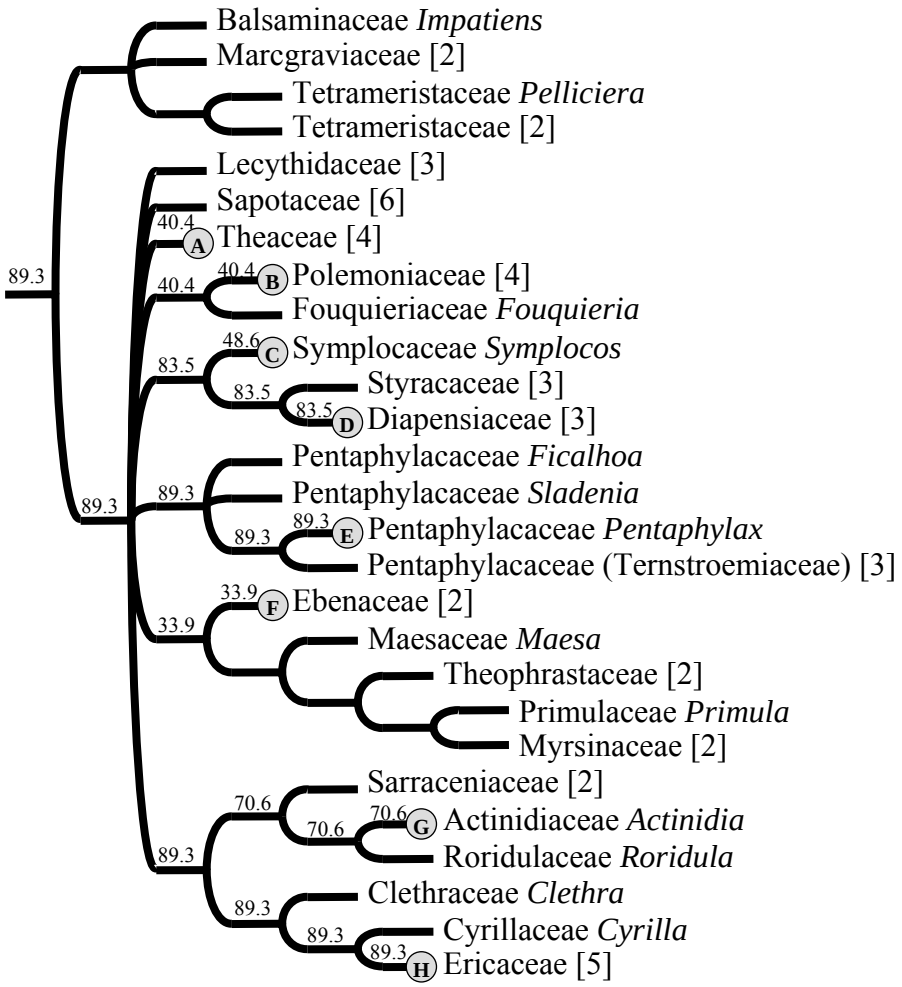


Figure 1.3. Minimum age dating of the Ericales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Schönenberger et al. (2005). A- *Gordonia lamkinensis*, Middle Eocene (40.4 mya). B- *Gilisenium hueberi*, Lutetian-Bartonian (40.4 mya). C- *Symplocos grimsleyi*, Ypresian (48.6 mya). D- *Actinocalyx bohrii*, Late Santonian-Early Campanian (83.5 mya). E- *Pentapetalum trifasciculandricus*, Turonian (89.3 mya). F- *Austrodiospyros cryptostoma*, Late Eocene (33.9 mya). G- *Parasaurauia allonensis*, Early Campanian (70.6 mya). H- *Paleoenkianthus sayrevillensis*, Turonian (89.3 mya).

Aquifoliales— This order *sensu* Bremer et al. (2002) includes only four families (Figure 1.4), of these, only Aquifoliaceae has a fossil record (Table 1.5), starting with Maastrichtian fruits mentioned by Knobloch and Mai (1986) and Paleocene fruits reported by Mai (1987). Brown (1962) reported some leaves from the Early Tertiary of Colorado, however, Collinson et al. (1993) have pointed out the need for a critical revision of the these leaves. Pollen belonging to *Ilexpollenites* has been reported from the Late Cretaceous of South Australia (Martin, 1977).

Table 1.5. Early fossil record of the Aquifoliales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Aquifoliaceae					
Ilex antiqua Knobloch et Mai 1986	fruit	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	no
Ilex gonnensis Mai 1970	seed	Late Paleocene	Gonna, Germany	Mai, 1987	yes
Ilex hercynica Mai 1970	seed	Early Paleocene	Gonna, Germany	Mai, 1987	yes
Ilex	pollen	Middle Oligocene	Sn Sebastián, Puerto Rico	Graham and Jarzen, 1969	no
Ilexpollenites	pollen	Campanian	San Joaquín Valley, CA, USA	Martin, 1977	no

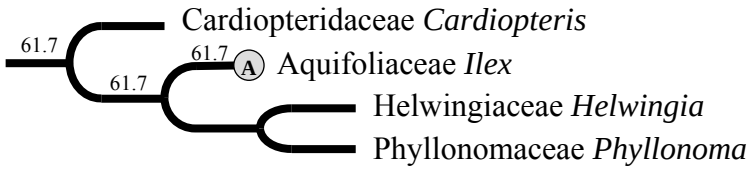


Figure 1.4. Minimum age dating of the Aquifoliales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Bremer et al. (2002). A- *Ilex hercynica*, Early Paleocene (61.7 mya).

Apiales— Seven families compose this order in the Bremer et al. (2002) cladogram; Apiaceae, Araliaceae, Aralidiaceae, Torriceliaceae, Melanophyllaceae, Griseliniaceae, and Pittosporaceae, of which three have been reported from the fossil record (Table 1.6). The more comprehensive analysis of Chandler and Plunkett (2004) confirms these families as Apialean lineages and also segregates some members of Apiaceae and Araliaceae, the *Mackinlaya* and the *Myodocarpus* groups (Figure 1.5).

Torricelliaceae has representatives in the Eocene of Washington, Oregon and Germany and the Miocene of Austria (Table 1.6). Araliaceae has an extensive fossil record that goes back to the Late Cretaceous but that is in need of revision; few of the araliaceous fossils can be considered reliable and revising them would be of extreme importance. As of now, the oldest reliable record are the leaves of *Dendropanax* described by Dilcher and Dolph (1970) from the Eocene of Tennessee and fruits of *Paleopanax* Manchester (1994) from the Eocene of Oregon (Table 1.6, Figure 1.5).

Table 1.6. Early fossil record of the Apiales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Torricelliaceae					
Torricellia bonesii (Man_ chester) Manchester 1999	fruit	Early Miocene	Oberdorf, Austria	Manchester, 1999	yes
Torricellia bonesii (Man_ chester) Manchester 1999	fruit	Middle Eocene	Roslyn, Washington	Manchester, 1999	yes
Torricellia bonesii (Man_ chester) Manchester 1999	fruit	Middle Eocene	Clarno, OR, USA	Manchester, 1999	yes
Torricellia bonesii (Man_ chester) Manchester 1999	fruit	Middle Eocene	Messel, Germany	Manchester, 1999	yes
Araliaceae ("Apiaceae")					
Hydrocotyle sp Łańcucka-Środoniowa 1979	fruit	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_ doniowa, 1979	yes
Araliaceae					
Aralia antiqua Knobloch et Mai 1986	endo_ carp	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	no

Table 1.6. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Aralia cf. *ucrainica* Dorofeev 1963	endo_carp	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_doniowa, 1979	yes
Aralia rugosa Dorofeev 1963	endo_carp	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_doniowa, 1979	yes
Aralia tertiaria Dorofeev 1963	endo_carp	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_doniowa, 1979	yes
Acanthopanax fiedrichii Knobloch et Mai 1986	endo_carp	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	no
Acanthopanax gigantocarpus Knobloch et Mai 1986	endo_carp	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	no
Acanthopanax mansfeldensis Knobloch et Mai 1986	endo_carp	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	no
Acanthopanax obliquocostatus Knobloch et Mai 1986	endo_carp	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	no
Dendropanax eocenensis Dilcher et Dolph 1970	leaf	Middle Eocene	Claiborne, TN, USA	Dilcher and Dolph, 1970	yes
Dendropanax	pollen	Middle Oligocene	Sn Sebastián, Puerto Rico	Graham and Jarzen, 1969	no
Oreopanax dakotensis Melchior 1976	fruit	Paleocene	Wannagan Creek Flora, ND, USA	Melchior, 1976	no
Paleopanax oregonensis Manchester 1994	endo_carp	Middle Eocene	Clarno, Oregon	Manchester, 1994	yes
Schefflera dorofeevii Łańcucka-Środoniowa 1975	endo_carp	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	no

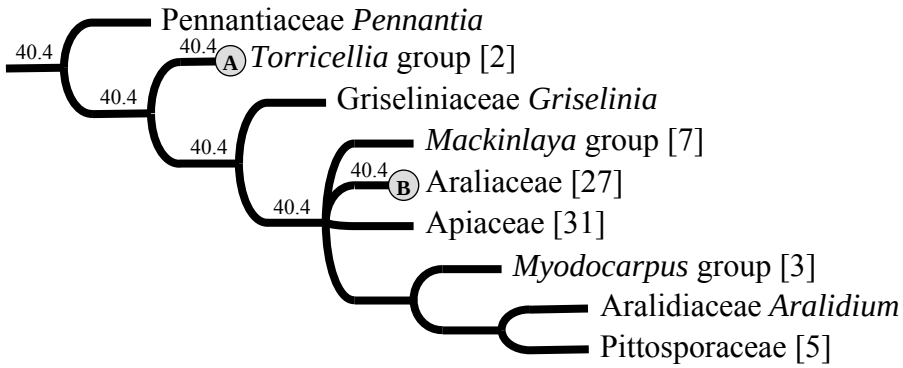


Figure 1.5. Minimum age dating of the Apiales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Chandler and Plunkett (2004). A- *Torricellia bonesii*, Middle Eocene (40.4 mya). B- *Dendropanax eocenensis*, Middle Eocene (40.4 mya).

Escalloniaceae-Paracryphiaceae— In the Bremer et al. (2002) analysis, Escalloniaceae is resolved as polyphyletic, with *Escallonia*, *Tribeles* and *Polyosma* in one clade along with the Eremosynaceae (the newly recognized Order Escalloniales of APG [2009]), and Paracryphiaceae and *Quintinia* in a second clade, sister to the Dipsacales (the Order Paracryphiales of APG [2009]). The uncertainty about the relationships within the family makes it difficult to place fossils in proper context. However, fossil pollen from the Upper Eocene of New Zealand has been related to the genus *Quintinia* (Mildenhall, 1980), as have fusainized fossil flowers from the Late Santonian-Early Campanian of Southern Sweden (Friis, 1990).

Silvianthemum suecicum, the flower-based taxon from Sweden, was not put in phylogenetic context when described but it is still considered by its authors to be related to *Quintinia* (Friis et al., 2006). In one attempt to assess its phylogenetic relationships, Backlund (1996) added it to the Dipsacales matrix analyzed by

Backlund and Donoghue (1996) concluding that *Silvianthemum* occupied "a stable but not strongly supported position … just outside the basal node of the Dipsacales", although it is shown as sister to a Dipsacales-Apiales clade that also includes *Tribeles*, *Polyosma* and Bruniaceae, a result not fully compatible with current hypotheses of Campanuliid (Euasterid II) relationships. For this reason, a new analysis was performed using a fixed backbone based on the analyses by Bremer et al. (2002), Zhang et al. (2003) and Donoghue et al. (2003); the 58 taxa and characters 32-60 of the Backlund and Donoghue (1996) morphology matrix; and the Friis (1990) description of *Silvianthemum* to code its characters. Details of this analysis can be found in Appendix B. The strict consensus places *Silvianthemum* as sister to *Quintinia* with dorsifixed anther attachment as synapomorphy (Figure 1.6). Although under the current phylogenetic framework, *Silvianthemum* is better placed with *Quintinia*, this might change when the phylogenetic relationships among members of the apparently polyphyletic Escalloniaceae are better understood.

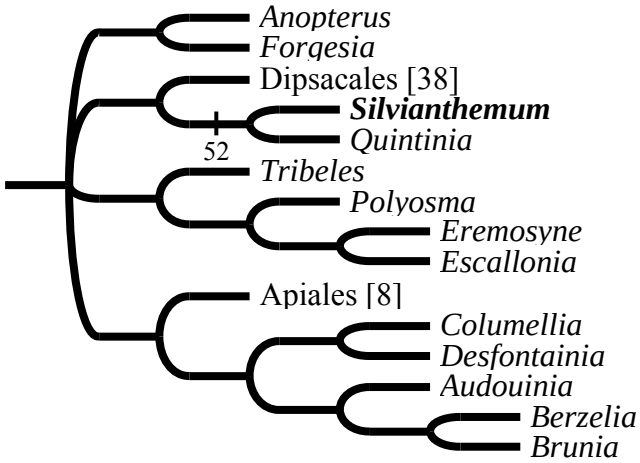


Figure 1.6. Strict consensus of 312 trees (L=204, CI=32, RI=68) showing the position of the fossil *Silvianthemum* as sister to *Quintinia* with dorsifixed anther attachment (ch 52) as synapomorphy (see Appendix B for details). Numbers in brackets indicate number of descendant terminals.

Dipsacales— Several fossils have been described as leaves of *Viburnum*, however many are dubious and many have been shown to represent different taxa; for example, those described by Brown (1962) were transferred to *Davidia* of the Cornales (Manchester, 2002). The macrofossil record of the Dipsacales was reviewed by Manchester and Donoghue (1995) and several reports that were rejected by those authors have not been included here (i.e. fossils formerly referred to *Abelia*). Bell and Donoghue (2005) have also evaluated the available fossil record of the Dipsacales when searching for suitable calibration points for their molecular age estimation analysis and found that *Diplodipelta* is the oldest most reliable fossil of this group. *Diplodipelta* places the Dipsacales in the Late Eocene (Table 1.7, Figure 1.7) and although it was not placed in phylogenetic analysis as a terminal, enough synapomorphies were found to confidently place it as sister of *Dipelta* (Manchester and Donoghue, 1995).

Table 1.7. Early fossil record of the Dipsacales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Adoxaceae					
Sambucus	seed/ fruit	Middle Eocene	Messel, Germany	Collinson, 1988	no
Sambucus	leaf	Late Eocene	Florissant, CO, USA	Manchester, 2001	no
Caprifoliaceae ("Diervillaceae")					
Diervilla echinata Piel 1971	pollen	Oligocene	Fraser River, BC, Canada	Piel, 1971	yes
Caprifoliaceae					
"Caprifoliaceae"	seed/ fruit	Middle Eocene	Clarno, OR, USA	Bones, 1979	no
Symphoricarpos elegans (Lesquereux) Smith 1937	leaf	Eocene	Ruby River Basin, MT, USA	Becker, 1961	no
Linnaeaceae					
Dipelta europaea Reid et Chandler 1926	fruit	Late Eocene-Early Oligocene	Bembridge, UK	Reid and Chandler, 1926	yes

Table 1.7. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Diplodipelta miocenica (Berry) Manchester et Donoghue 1995	fruit	Miocene	Succor Creek, WA, ID, OR, USA	Manchester and Donoghue, 1995	yes
Diplodipelta reniptera (Becker) Manchester et Donoghue 1995	fruit	Late Eocene-Oligocene	Florissant, Mormon Cr, Ruby, CO, MT, USA	Manchester and Donoghue, 1995	yes

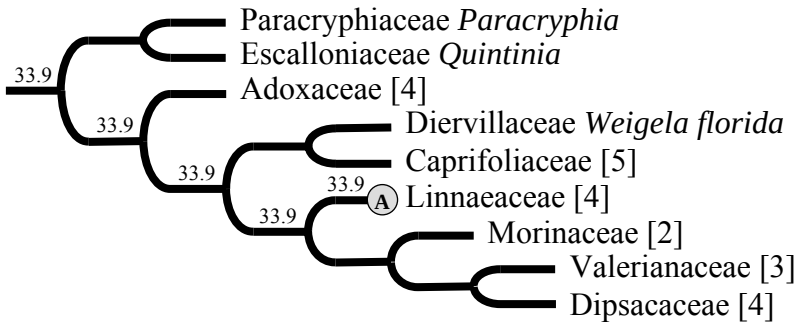


Figure 1.7. Minimum age dating of the Dipsacales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Zhang et al. (2003). A- *Diplodipelta reniptera*, Late Eocene-Oligocene (33.9 mya).

Asterales— The most recent phylogenetic study of the Asterales is that of Lundenberg and Bremer (2003) where they include 12 families in the order. Few of these are represented in the fossil record; macrofossil records include seeds assigned to Campanulaceae and Menyanthaceae (Table 1.8), a stem assigned to *Donatia* (Donatiaceae or Stylidaceae) and fruits assigned to Asteraceae (Table 1.8). In this group, the pollen record is more extensive than the macrofossil one, with families like Stylidaceae *s.s.* and Goodeniaceae known only from fossil pollen.

The fossil record of the Asteraceae, one of the most species-rich families of flowering plants, has been elusive. Graham, in 1996, reviewed the available fossil record up to that point, however, that information is now outdated. In 2000, Zavada and de Villiers reported pollen grains of the tribe Mutisiae from South Africa and assigned them the name *Tubulifloridites antipodica* (Table 1.8). These pollen grains were assigned a Late Paleocene-Eocene age and became the oldest fossils for the family and for the order. But Scott et al. (2006) cast doubts on their identity suggesting that the South African *T. antipodica* is probably conspecific with *T. viteauensis*, a second taxon described by Zavada and deVilliers (2000) from Middle Eocene (Bartonian) sediments (Scott et al., 2006) offshore the coast of Namibia (Table 1.8, Figure 1.8).

Many reports of asteraceous macrofossils have been discredited: *Cypselites* has been reinterpreted as representing seeds of Apocynaceae instead of achenes of Asteraceae (Reid and Chandler, 1926; Manchester, 2001), *Viguiera cronquistii* had no characters linking it definitely to the Asteraceae (Crepet and Stuessy, 1978) and *Parthenites priscus* is not even a real fossil (pers. obs).

Table 1.8. Early fossil record of the Asterales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Campanulaceae					
Campanula palaeopyramidalis Łańcucka-Środoniowa 1977	seed	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Środoniowa, 1977	yes
Campanula sp. Łańcucka-Środoniowa 1979	seed	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Środoniowa, 1979	yes

Table 1.8. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Stylidiaceae					
Tricolpites stylidioides Macphail et Hill 1994	pollen	Early Oligocene	Lemonthyme Creek, NW Tasmania	Macphail and Hill, 1994	no
Donatia novae-zelandiae Hook f. 1853	stem	Pleistocene	Comstock, King River Valley, Tasmania	Gibson et al., 1987	yes
Menyanthaceae					
Menyanthes cf. *trifoliata* L 1753	seed	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_ doniowa, 1979	yes
Striasyncolpites laxus Mildenhall et Pocknall 1989	pollen	Late Oligocene-Middle Miocene	Cullen, Tierra del Fuego, Argentina	Zamaloa, 2000	no
Goodeniaceae					
Poluspissusites digitatus Salard-Cheboldaeff 1978	pollen	Oligocene	Kwa-Kwa, Cameroon	Salard-Cheboldaeff, 1978	yes
Asteraceae					
Cypselites aquensis Saporta 1889	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1889	no
Cypselites fractus Saporta 1889	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1889	no
Cypselites gypsorum Saporta 1861	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1862	no
Cypselites philiberti Saporta 1872	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1873	no
Cypselites spoliatus Saporta 1889	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1889	no
Cypselites stenocarpus Saporta 1872	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1873	no
Cypselites tenuirostratus Saporta 1889	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1889	no
Cypselites trisulcatus Saporta 1889	fruit	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1889	no
Hieracites nudatus Saporta 1889	head	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1889	no
Hieracites salyorum Saporta 1861	leaf	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1862	no
Hieracites stellatus Saporta 1889	head	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1889	no
Mutisiapollis patersonii Macphail et Hill 1994	pollen	Early Oligocene	Lemonthyme Creek, NW Tasmania	Macphail and Hill, 1994	yes

Table 1.8. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Parthenites priscus Saporta 1861	leaf	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1862	no
Tubulifloridites antipodica Cookson ex Potonie 1960	pollen	Late Paleocene-Eocene	Koingnaas, South Africa	Zavada and de Villiers, 2000	yes
Tubulifloridites viteauensis Barreda 1993	pollen	Eocene	Shearwater Bay, South Africa	Zavada and de Villiers, 2000	yes
Viguiera cronquistii Becker 1969	head	Late Oligocene-Early Miocene	Beaverhead Basin, sw MT, USA	Crepet and Stuessy, 1978	no
"Asteraceae"	fruit	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	no

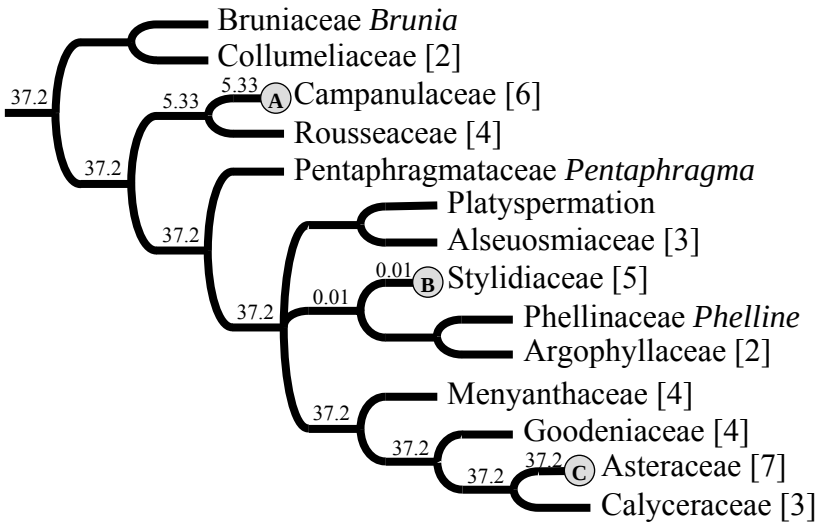


Figure 1.8. Minimum age dating of the Asterales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Lundenberg and Bremer (2003). A- *Campanula palaeopyramidalis*, Miocene (5.33 mya). B- *Donatia novae-zelandiae*, Pleistocene (0.01 mya). C- *Tubulifloridites viteauensis* (37.2 mya).

Oncothecaceae-Icacinaceae— In the Bremer et al. (2002) analysis, the Icacinaceae turned out as polyphyletic, with *Apodytes* as sister to *Oncotheca* in one clade and *Cassinopsis*, *Icacina* and *Pyrenacantha* in a different clade, more closely related to the rest of the Lamiid groups than to the *Apodytes* clade (Figure 1.1). This partly agrees with the results of Kårehed (2001) who recovered a Garryales-*Apodytes* group and a separate *Icacina* group. This condition makes it difficult to assign some fossils to particular clades, especially when the fossil is of a genus not represented in the phylogenetic analysis. As of today, the position and relationships of the members of Icacinaceae are still unresolved and fluctuating (APG, 2009). For example, in the analysis of Soltis et al. (2007), the only member of Icacinaceae included, *Icacina*, was recovered as sister to a clade that includes all Lamiid groups except a clade Garryales-*Oncotheca*. This contrasts with the analysis of Bremer et al. (2002) where the *Icacina* would be sister to all other Lamiids including Garryales but not *Oncotheca*.

The earliest reproductive structures assigned to the Icacinaceae *s.l.* are the endocarps of *Iodes germanica* from the Maastrichtian of Germany (Table 1.9) while the earliest vegetative structures seem to go back to the Late Albian with the fossil wood *Icacinoxylon* (Table 1.9). Collinson et al. (1993), however, cast doubts on the identity of these woods and suggest the need for a revision. A review of fossil endocarps of the Icacinaceae is found in Pigg et al (2008).

Table 1.9. Early fossil record of the clades Oncotheca-Icacinaceae and Icacinaceae.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Icacinaceae					
Calatoloides eocenicum Berry 1922	fruit	Eocene	Wilcox, TX, USA	Berry, 1922	no

Table 1.9. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Goweria bibaiensis Tanai 1990	leaf	Middle Eocene	Hokkaido, Japan	Tanai, 1990	yes
Hosiea marchiaca Mai 1987	endo_ carp	Middle Paleocene	Nanjemoy, VA, USA	Tiffney, 1999	yes
Hosiea pterojugata Mai 1987	endo_ carp	Late Paleocene	Nanjemoy, VA, USA	Tiffney, 1999	yes
Huziokaea eoutilus (Endo) Tanai 1990	leaf	Late Eocene	Hokkaido, Japan	Tanai, 1990	yes
Icacinicarya dictyota Pigg, Manchester et DeVore	endo_ carp	Late Paleocene	Beicegel Creek, ND, USA	Pigg et al., 2008	yes
Icacinicarya collinsonae Pigg, Manchester et DeVore	endo_ carp	Late Paleocene	Almont, ND, USA	Pigg et al., 2008	yes
Icacinicaryites corruga (Brown) Pigg, Manchester et DeVore	endo_ carp	Late Paleocene	USGS 9492, CO, USA	Pigg et al., 2008	yes
Icacinicaryites linchensis Pigg, Manchester et DeVore	endo_ carp	Late Paleocene	Linch WY, USA	Pigg et al., 2008	yes
Icacinoxylon alternipunctata Wheeler, Lee et Matten 1987	wood	Maastrichtian	McNairy Fm, IL, USA	Wheeler et al., 1987	yes
Icacinoxylon pittiense Thayn, Tidwell et Stokes 1985	wood	Late Albian	Cedar Mountain, UT, USA	Thayn et al., 1985	no
Iodes germanica Knobloch et Mai 1986	endo_ carp	Maastrichtian	Eisleben, Germany	Knobloch and Mai, 1986	yes
Iodes multireticulata Reid et Chandler 1933	endo_ carp	Early Ypresian, Early Eocene	Nanjemoy, VA, USA	Tiffney, 1999	yes
Iodes multireticulata Reid et Chandler 1933	endo_ carp	Middle Eocene	Clarno, Oregon, USA	Manchester, 1994	yes
Iodes multireticulata Reid et Chandler 1933	fruit	Early Eocene	London Clay, England	Reid and Chandler, 1933	yes
Merrilliodendron ezoanum Tanai 1990	leaf	Late Eocene	Hokkaido, Japan	Tanai, 1990	yes
Phytocrene microcarpa Scott et Barghoorn 1957	fruit	Early Late Cretaceous	Raritan, NY, USA	Scott and Barghoorn, 1957	yes
Phytocrene ozakii Tanai 1990	leaf	Late Eocene	Hokkaido, Japan	Tanai, 1990	yes
Pyrenacantha sp	leaf	Late Eocene	Hokkaido, Japan	Tanai, 1990	yes

Garryales— Despite the small size of this clade –only of two families, Garryaceae (including *Aucuba*) and Eucommiaceae (Bremer et al., 2002)–, the fossil record is somewhat extensive. Garryaceae has been reported from the Miocene (Table 1.10). Eucommiaceae, on the other hand, is well documented from the fossil record starting from the Late Early Eocene (Table 1.10, Figure 1.9) which underwent revision by Call and Dilcher (1997), Manchester (1999) and Manchester et al. (2009).

Table 1.10. Early fossil record of the Garryales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Garryaceae					
Garrya axelrodi Wolfe 1964	leaf	Late Miocene	Stewart Spr, NV, USA	Wolfe, 1964	yes
Eucommiaceae					
Eucommia cf. *E. ulmoides* Leopold and Clay-Poole 2001	pollen	Late Eocene	Florissant, CO, USA	Leopold and Clay-Poole, 2001	yes
Eucommia constans Magallón-Puebla et Cevallos-Ferriz 1994	fruit	Early Oligocene	Pie de Vaca, Pue, Mexico	Magallón-Puebla and Cevallos-Ferriz, 1994	yes
Eucommia eocenica (Berry) Brown 1940	fruit	Middle Eocene	Claiborne, Tenn, USA	Call and Dilcher, 1997	yes
Eucommia jeffersonensis Call et Dilcher 1997	fruit	Late Eocene	Lower John Day OR USA	Call and Dilcher, 1997	yes
Eucommia kobayashii Huzioka 1961	fruit	Eocene	Yubari, Hokkaido, Japan	Huzioka, 1961	yes
Eucommia montana R. W. Brown 1940	fruit	Late Eocene	Florissant, CO, USA	Manchester, 2001	no
Eucommia montana R. W. Brown 1940	fruit	Late Early Eocene	Republic, WA, USA	Call and Dilcher, 1997	yes
Eucommia rolandii Call et Dilcher 1997	leaf	Middle Eocene	Talahatta, Holly Spr, MS, USA	Call and Dilcher, 1997	yes
Eucommia ulmoides Oliv 1890	fruit	Late Miocene (Tortonian)	Poland	Szafer, 1961	yes
Tricolpites sp. cf. Eucommia	pollen	Late Paleocene	Powder River Basin, WY, MT, USA	Pocknall, 1987b	no

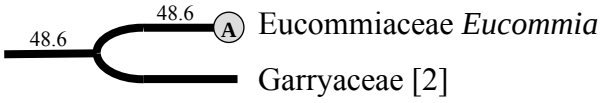


Figure 1.9. Minimum age dating of the Garryales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Bremer et al. (2002). A- *Eucommia montana*, Late Early Eocene (48.6 mya).

Gentianales— The fossil record of this order, which contains two of the most species-rich families of angiosperms, dates back to the Early Tertiary, probably Paleocene but most likely Eocene (Table 1.11, Figure 1.10). In a preliminary survey of the Black Peaks Formation from the Paleocene of Texas, Abbott (1986) mentioned the presence of wood of Rubiaceae, however it was never described. Graham (2009), who recently reviewed the fossil record of the Rubiaceae also accepts *Emmenopterys* as one of the its oldest members (Table 1.11). Fossils identified as Apocynaceae are relatively common in the Early Oligocene of England (Table 1.11) and probably elsewhere in Europe if the reports of *Cypselites* are proven to be apocynaceous (Reid and Chandler, 1926; Manchester, 2001). Woods from the Maastrichtian with affinities to the Apocynaceae were described by Wheeler et al. (1987), however, formal assignation to the family was never made. Gentianaceae has been reported from the Eocene (Table 1.11) based on a preserved flower and the pollen contained in it, however, in spite of the very distinctive pollen the paucity of other floral characters casts some doubt on this identification (Crepet, pers. comm.).

Table 1.11. Early fossil record of the Gentianales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Rubiaceae					
Emmenopterys dilcheri Manchester 1994	fruit	Middle Eocene	Clarno, OR, USA	Manchester, 1994	yes
Faramea	pollen	Middle Oligocene	Sn Sebastián, Puerto Rico	Graham and Jarzen, 1969	no
Remijia tenuiflorifolia Berry 1938	leaf	Lutetian (Middle Eocene)	Laguna del Hunco, Argentina	Rodríguez de Sarmiento and Durango de Cabrera, 1995	no
Retitricolporites annulatus Salard-Cheboldaeff 1978	pollen	Oligocene-Early Miocene	Kwa-Kwa, Cameroon	Salard-Chebol_ daeff, 1978	yes
"Rubiaceae"	wood	Paleocene	Black Peaks Fm, TX, USA	Abbott, 1986	no
Loganiaceae					
"Loganiaceae"	pollen	Pliocene	Cerro la Popa, Colombia	Sole de Porta, 1960	no
Gentianaceae					
Pistillipollenites mcgregorii Rouse	pollen	Early Eocene	Wasatch Fm, WY, USA	Pocknall, 1987	no
Voyrioseminites magnus Trivedi and Chaturvedi 1972	seed	Eocene	Kuala Lumpur, Malaysia	Trivedi and Chaturvedi, 1972	yes
"Gentianaceae"	flower	Early Eocene	Wilcox, TX, USA	Crepet and Daghlian, 1981	yes
Apocynaceae					
Apocynophyllum helveticum Heer 1859	leaf	Middle Eocene	Messel, Germany	Wilde, 1989	yes
Apocynospermum dubium Reid et Chandler 1926	seed	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Apocynospermum elegans Reid et Chandler 1926	seed	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Apocynospermum rostratum Reid et Chandler 1926	seed	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Apocynospermum striatum Reid et Chandler 1926	seed	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Apocynospermum	seed	Late Eocene	Florissant, CO, USA	Manchester, 2001	no
Brevicolporites molinae (Schuler et Doubinger) Salard-Cheboldaeff 1978	pollen	Oligocene-Early Miocene	Kwa-Kwa, Cameroon	Salard-Chebol_ daeff, 1978	yes
Echitonium ashczisaicum Vassiljev 1976	leaf	Early Tertiary	Aktyubinsk, Kazakhstan	Vassiljev, 1976	yes
Echitonium sophiae O. Web 1852	leaf	Early Tertiary	Aktyubinsk, Kazakhstan	Vassiljev, 1976	yes

Table 1.11. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Euholarrhenoxylon aisnense Gros 1993	wood	Lutetian	Aisne valley, France	Gros, 1993	yes
Paraapocynaceoxylon barghoorni Wheeler, Lee et Matten 1987	wood	Maastrichtian	McNairy Fm, Illinois	Wheeler et al., 1987	yes
Phyllantera vectensis Reid et Chandler 1926	seed	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Rauwolfia	pollen	Middle Oligocene	Sn Sebastián, Puerto Rico	Graham and Jarzen, 1969	no
Tabernaemontana cf. *T. coronaria* Leopold and Clay-Poole 2001	pollen	Late Eocene	Florissant, CO, USA	Leopold and Clay-Poole, 2001	yes
Apocynaceae ("Asclepiadaceae")					
Polyporotetradites laevigatus Salard-Cheboldaeff 1978	pollen	Oligocene-Early Miocene	Kwa-Kwa, Cameroon	Salard-Chebol_ daeff, 1978	yes

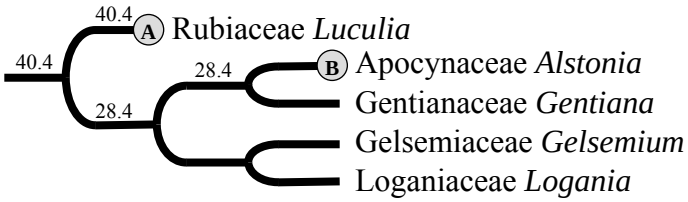


Figure 1.10. Minimum age dating of the Gentianales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Bremer et al. (2002). A- *Emmenopterys dilcheri*, Middle Eocene (40.4 mya). B- *Apocynospermum rostratum*, Early-Middle Oligocene (28.4 mya).

Vahliaceae-Boraginaceae— In the analysis of Bremer et al. (2002), Vahliaceae and Boraginaceae form a clade (Figure 1.1), however this arrangement is different in other analyses (e.g. Soltis et al., [2007]). The fossil record of the Boraginaceae is restricted to the Tertiary starting in the Early Eocene (Table 1.12;

Figure 1.11). Boraginaceous seeds were reported from India (Table 1.12) and assigned a Paleocene age based on the presence of these same seeds, this age assignment was arbitrary and cannot be considered reliable.

Two fusainized flowers from the Late Cretaceous of Sweden, *Scandianthus major* and *S. costatus*, were originally described as belonging to the Saxifragalean complex and compared to Hydrangeaceae, Vahliaceae, Escalloniaceae and Saxifragaceae (Friis and Skarby, 1982; Friis, 1984). Subsequent phylogenetic analyses spanning all of the angiosperms have shown that those families are not closely related. Nevertheless, the authors have maintained the fossils close to the Vahliaceae (Friis et al., 2006) despite the fact that they had not been subject to phylogenetic analysis or had their characters reviewed in light of more recent phylogenetic hypotheses (Hermsen et al 2006). For this reason, the comparison table included in the protologue of *Scandianthus* was adapted for phylogenetic analysis using a fixed backbone compatible with recent hypotheses of angiosperm relationships -Soltis et al. (2000), Bremer et al. (2002) and APG (2003). The final matrix has 12 morphological characters, 28 families and the fossil genus *Scandianthus*. In this analysis *Scandianthus* was resolved as sister taxa to Vahliaceae with one locule and pendant placenta as synapomorphies (Figure 1.12). Details of this analysis can be found in the Appendix C.

Table 1.12. Early fossil record of the Vahliaceae-Boraginaceae clade.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Vahliaceae					
Scandianthus costatus Friis et Skarby 1982	flower	Late Santonian-Early Campanian	Asen, Scania, S Sweden	Friis and Skarby, 1982	yes
Scandianthus major Friis et Skarby 1982	flower	Late Santonian-Early Campanian	Asen, Scania, S Sweden	Friis and Skarby, 1982	yes

Table 1.12. (Continued)

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Boraginaceae					
Cordia amurensis (Kryshtofovich et Baikovskaya) Chelebajeva 1984	leaf	Paleogene	Kamchatka, Russia	Chelebayeva, 1984	yes
Cordia congerminalis (Hollick) Chelebajeva 1984	leaf	Paleogene	Kamchatka, Russia	Chelebayeva, 1984	yes
Cordia kamtschatica Chelebajeva 1984	leaf	Paleogene	Kamchatka, Russia	Chelebayeva, 1984	yes
Cordia ochotensis Chelebajeva 1984	leaf	Paleogene	Kamchatka, Russia	Chelebayeva, 1984	yes
Cordia platanifolia (Ward) Chelebajeva 1984	leaf	Paleogene	Kamchatka, Russia	Chelebayeva, 1984	yes
Ehretia clausentia Chandler 1961	fruit	Early Eocene	London clay, England	Chandler, 1964	yes
Lithospermum dakotense Gabel 1987	fruit	Late Miocene	Ash Hollow, Bennett, SD, USA	Gabel, 1987	yes
Tournefortia	pollen	Middle Oligocene	San Sebastián Puerto Rico	Graham and Jarzen, 1969	no
"Boraginaceae"	seed	Paleocene?	Lameta Beds of Gujarat, India	Mathur and Mathur, 1985	no

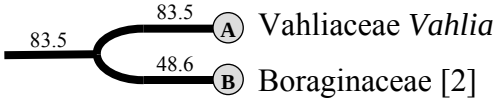


Figure 1.11. Minimum age dating of the Vahliaceae-Boraginaceae clade. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Bremer et al. (2002). A- *Scandianthus major*, Late Santonian-Early Campanian (83.5 mya). B- *Ehretia clausentia*, Early Eocene (48.6 mya).

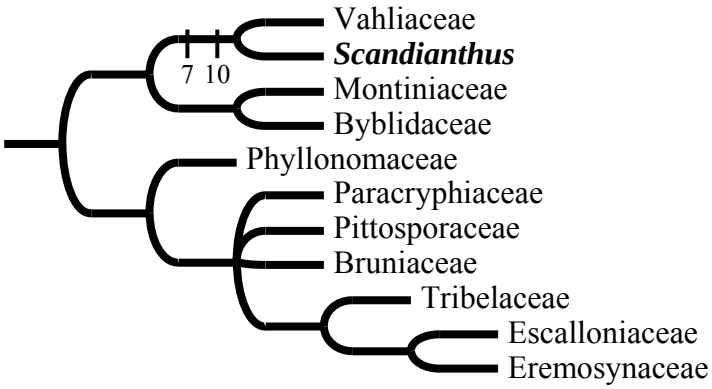


Figure 1.12. Part of the strict consensus of 32 trees (L=62, CI=22, RI=28) showing the position of the fossil genus *Scandianthus* as sister to Vahliaceae with one locule (ch 7) and pendant placentae (ch 10) as synapomorphies (see Appendix C for details and full tree).

Solanales— This clade is composed of five families in the cladogram of Bremer et al. (2002) and all of them have scarce or nonexistent fossil records based on existing literature. The Convolvulaceae fossil record is mostly represented by pollen; however there is a leaf from the Late Eocene (Table 1.13) that could be assigned to the group.

The Solanaceae, however, has had a few fossils assigned to it, although most of these reports have been unreliable due to poor preservation, poor descriptions, or poor comparative work (Table 1.13). *Cantisolanum daturoides* has frequently been cited as the oldest evidence for Solanaceae (i.e. Knapp, 2002), however, the taxon is only known from the type specimen, a seed which does not show enough characters to support its assignment to Solanaceae or to any other family (Collinson, 1983; pers. obs.). Several flowers assigned to Solanaceae from the Eocene of Eastern North America (Table 1.13) by Berry (1914, 1916, 1930) clearly do not show characters of this family and are therefore, also rejected (Martínez-Millán, unpubl.). The flower-

based taxon *Solanites brongniartii* from the Oligocene of France and the seed-based taxon *Solanispermum reniforme* from the Eocene of England (Table 1.13, Figure 1.13) show solanaceous characters and could potentially belong in this family. The oldest pollen record is probably that of *Datura* from the Late Eocene, although details about the structure of these grains were not provided (Table 1.13).

Table 1.13. Early fossil record of the Solanales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Convolvulaceae					
Convulvulites orichitus MacGinitie 1953	leaf	Late Eocene	Florissant, CO, USA	MacGinitie, 1953	yes
Merremia	pollen	Middle Oligocene	San Sebastián Puerto Rico	Graham and Jarzen, 1969	no
Tricolpites trioblatus Mildenhall et Pocknall 1989	pollen	Early-Middle Miocene	Etadunna, Lake Hydra, Australia	Martin, 2000	yes
Solanaceae					
Cantisolanum daturoides Reid et Chandler 1933	fruit	Early Eocene	London clay, England	Reid and Chandler, 1933	no
Datura cf. *D. discolor* Leopold and Clay-Poole 2001	pollen	Late Eocene	Florissant, CO, USA	Leopold and Clay-Poole, 2001	yes
Physalis pliocaenica Szafer 1947	fruit	Late Miocene (Tortonian)	Stare Gliwice, Poland	Szafer, 1961	no
Solanites brongniartii Saporta 1862	flower	Oligocene	Aix-en-Pro_ vence, France	Saporta, 1862	no
Solanites crassus Berry 1930	flower	Early Eocene	Claiborne, TN, USA	Berry, 1930	no
Solanites pusillus Berry 1930	flower	Early Eocene	Claiborne, TN, USA	Berry, 1930	no
Solanites saportanus Berry 1916	flower	Early Eocene	Claiborne, TN, USA	Berry, 1916	no
Solanites sarachaformis Berry 1930	flower	Early Eocene	Claiborne, TN, USA	Berry, 1930	no
Solanispermum reniforme Chandler 1957	seed	Eocene	Lower Bagshot, UK	Chandler, 1962	yes
Solanum arnense Chandler 1962	seed	Eocene	Lower Bagshot, UK	Chandler, 1962	yes
Solandra haeliadum Massalongo 1851	leaf	Eocene	Salcedo, Italy	Massalongo, 1851	no

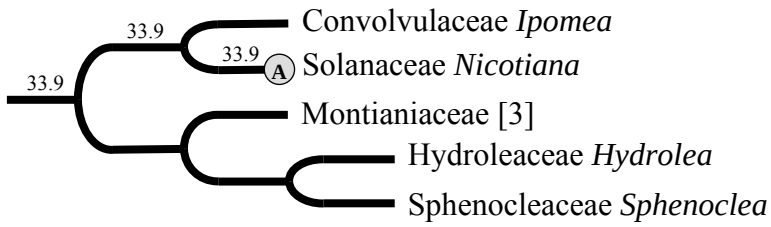


Figure 1.13. Minimum age dating of the Solanales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Bremer et al. (2002). A- *Solanispermum reniforme*, Eocene (33.9 mya).

Lamiales— Despite the size of this clade in terms of number of families (Bremer et al., 2002), the fossil record is sparse, with few examples from the Tertiary. Some isolated Eocene fossils had been reported in the past, however Collinson et al. (1993) reported most of these as unconfirmed or rejected them based on the poor preservation. Only one record of Oleaceae, *Fraxinus excelsior*, based on both reproductive and vegetative organs can be considered reliably supported by available evidence (Table 1.14, Figure 1.14). In the Plantaginaceae, Acanthaceae and Pedaliaceae, all of them with very scarce fossil records, there are only one or two reports which seem to be reliable (Table 1.14; Figure 1.14), while in the Bignoniaceae, a family a more extensive fossil record, around half of its reports should be considered unreliable. The Lamiaceae has been elusive in the fossil record; two fossils described by Cockerell (1926, 1927) were later rejected by MacGinitie (1969, 1953) leaving the fruits from the Bembridge flora in England, as the oldest fossils of this family (Table 1.14, Figure 1.14).

Table 1.14. Early fossil record of the Lamiales.

Fossil taxon	Organ	Age	Locality	Reference	Acc.
Oleaceae					
Fraxinus cf. *rupinarum* Becker 1961	fruit	Middle Eocene	Quilchena, BC, Canada	Mathewes and Brooke, 1971	no
Fraxinus excelsior L	leaf/ fruit	Late Miocene	Depresión Ceretana, Spain	Barrón, 1992	yes
Fraxinus leii Berry 1934	leaf	Maastrichtian	Lance Flora, SD, USA	Berry, 1934	no
Fraxinus rupinarum Becker 1961	fruit	Oligocene	Ruby River Basin, MT, USA	Becker, 1961	no
Plantaginaceae ("Scrophulariaceae")					
Gratiola tertiaria Łańcucka-Środoniowa 1977	seed	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_ doniowa, 1977	yes
Acanthaceae					
Acanthus rugatus Reid et Chandler 1926	seed	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Bignoniaceae					
Catalpa coloradensis (Axelrod) Wolfe et Schorn 1990	leaf	Oligocene	Creede Flora, CO, USA	Wolfe and Schorn, 1990	no
Catalpa rugosa Reid et Chandler 1926	seed	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Catalpa sp	leaf	Oligocene	Creede Flora, CO, USA	Wolfe and Schorn, 1989	no
Incarvillea pristina Reid et Chandler 1926	seeds	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Jacaranda	pollen	Middle Oligocene	Sn Sebastián, Puerto Rico	Graham and Jarzen, 1969	no
Radermachera pulchra Reid et Chandler 1926	seeds	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Tecoma	pollen	Middle Oligocene	Sn Sebastián, Puerto Rico	Graham and Jarzen, 1969	no
Verbenaceae					
Gmelina tertiara Bande 1986	wood	Paleogene	Deccan Intertrappean Beds, India	Bande, 1986	yes
Holmskioldia quilchenensis Mathewes et Brooke 1971	calyx	Middle Eocene	Quilchena, BC, Canada	Mathewes and Brooke, 1971	no
Holmskioldia speiri (Lesquereux) MacGinitie 1953	leaf/ fruit	Oligocene	Ruby River Basin, MT, USA	Becker, 1961	no

Table 1.14. (Continued).

Fossil taxon	Organ	Age	Locality	Reference	Acc.
"Verbenaceae"	wood	Paleocene	Black Peaks Fm, TX, USA	Abbott, 1986	no
Pedaliaceae					
Trapella cf. *antennifera* (Léveillé) Glück	fruit	Pliocene	Swisterberg, Germany	Tralau, 1965	yes
Trapella weylandi (Thomson et Grebe) Tralau 1964	fruit	Pliocene	Swisterberg/ Weilerswist, Germany	Tralau, 1964	yes
Lamiaceae					
Ajuginucula smithii Reid et Chandler 1926	fruit	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Lycopus cf. *antiquus* Reid 1920	fruit	Miocene	Nowy Sacz Basin, Poland	Łańcucka-Śro_ doniowa, 1979	yes
Melissa parva Reid et Chandler 1926	fruit	Early-Middle Oligocene	Bembridge, England	Reid and Chandler, 1926	yes
Menthites eocenicus Cockerell 1926	calyx	Eocene	Green River, CO, USA	Cockerell, 1926	no
Nepeta? pseudaeluri Cockerell 1927	leaf	Miocene	Florissant, CO, USA	Cockerell, 1927	no

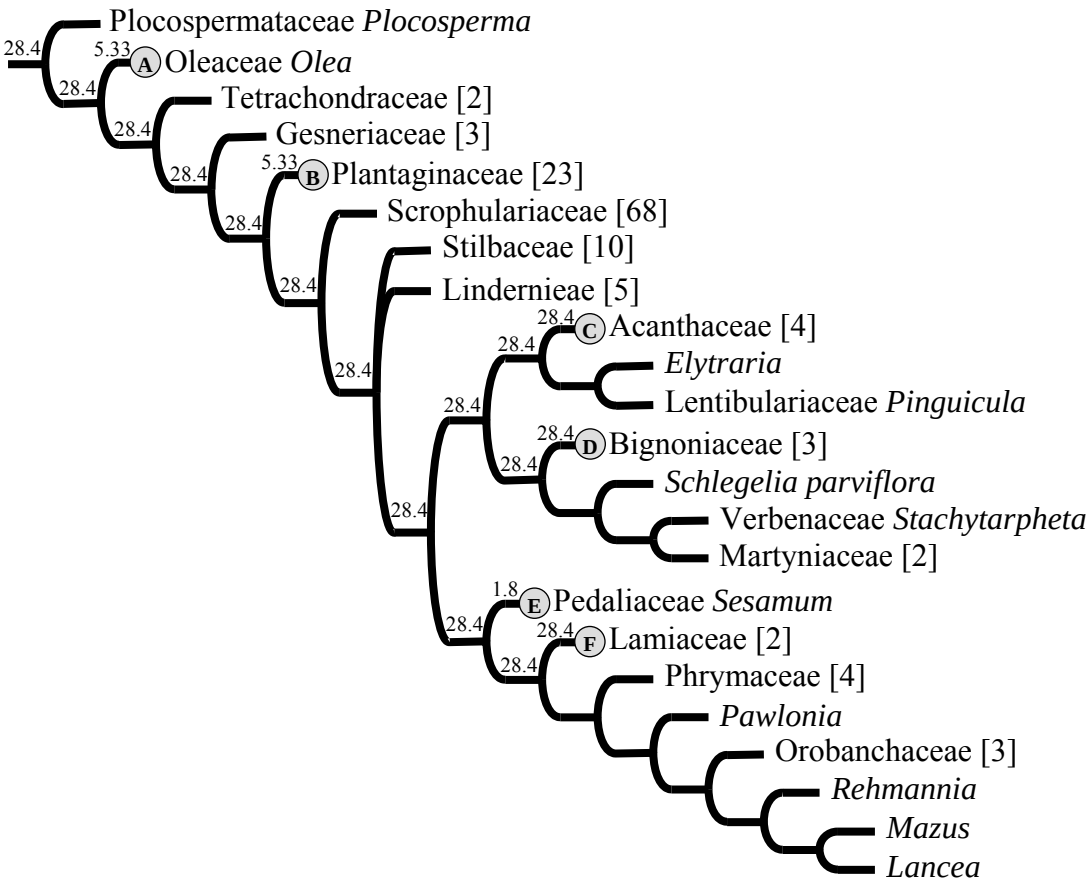


Figure 1.14. Minimum age dating of the Lamiales. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Oxelman et al. (2005). A- *Fraxinus excelsior*, Late Miocene (5.33 mya). B- *Gratiola tertiaria*, Miocene (5.33 mya). C- *Acanthus rugatus*, Early-Middle Oligocene (28.4 mya). D- *Radermachera pulchra*, Early-Middle Oligocene (28.4 mya). E- *Trapella weylandi*, Pliocene (1.8 mya). F- *Melissa parva*, Early-Middle Oligocene (28.4 mya).

Dating of the Asterid Tree— The estimated minimum age estimated for the whole of the Asteridae is the Turonian (Late Cretaceous), some 89.3 my ago (Table 1.15, Figure 1.15) with the oldest fossils appearing simultaneously in the Cornales and the Ericales (Table 1.15). The Euasteridae makes its appearance shortly after, in the Late Santonian-Early Campanian, some 83.5 my ago (Table 1.15, Figure 1.15) when the oldest fossils of its two clades, the lamiids and the campanulids, make their first appearances simultaneously (Table 1.15, Figure 1.15). Diversification within these two clades took place shortly after. By the Eocene, most orders were present in the fossil record. Only Lamiales diversified later, in the Oligocene (Table 1.15, Figure 1.15).

Table 1.15. Estimated times of divergence of relevant angiosperm groups based on fossil estimates and molecular dating, ages are given in millions of years before present (MYBP).

Clade	Magallón et al., 1999	Wikström et al., 2001	Bremer et al., 2004	Crepet et al., 2004	this work
Estimate	fossil	molecular	molecular	fossil	fossil
Angiosperms	---	158-179	---	113	---
Eudicots	---	131-147	---	100	---
Asterids	---	112-122	---	90	89.3
Cornales	69.5	106-114	128	---	89.3
Ericales	89.5	106-114	127	90	89.3
Euasterids	---	107-117	127	---	83.5
Campanulids	---	102-112	123	---	83.5
Aquifoliales	69.5	99-107	121	---	61.7
Apiales	69.5	85-90	113	---	40.4
Dipsacales	53.2	85-90	111	---	33.9
Asterales	29.3	101-94	112	---	37.2
Lamiids	---	102-112	123	---	83.5
Garryales	45.9	100-107	114	---	48.6
Gentianales	53.2	83-89	108	---	40.4
Solanales	53.2	82-86	106	---	33.9
Lamiales	37	71-74	106	---	28.4

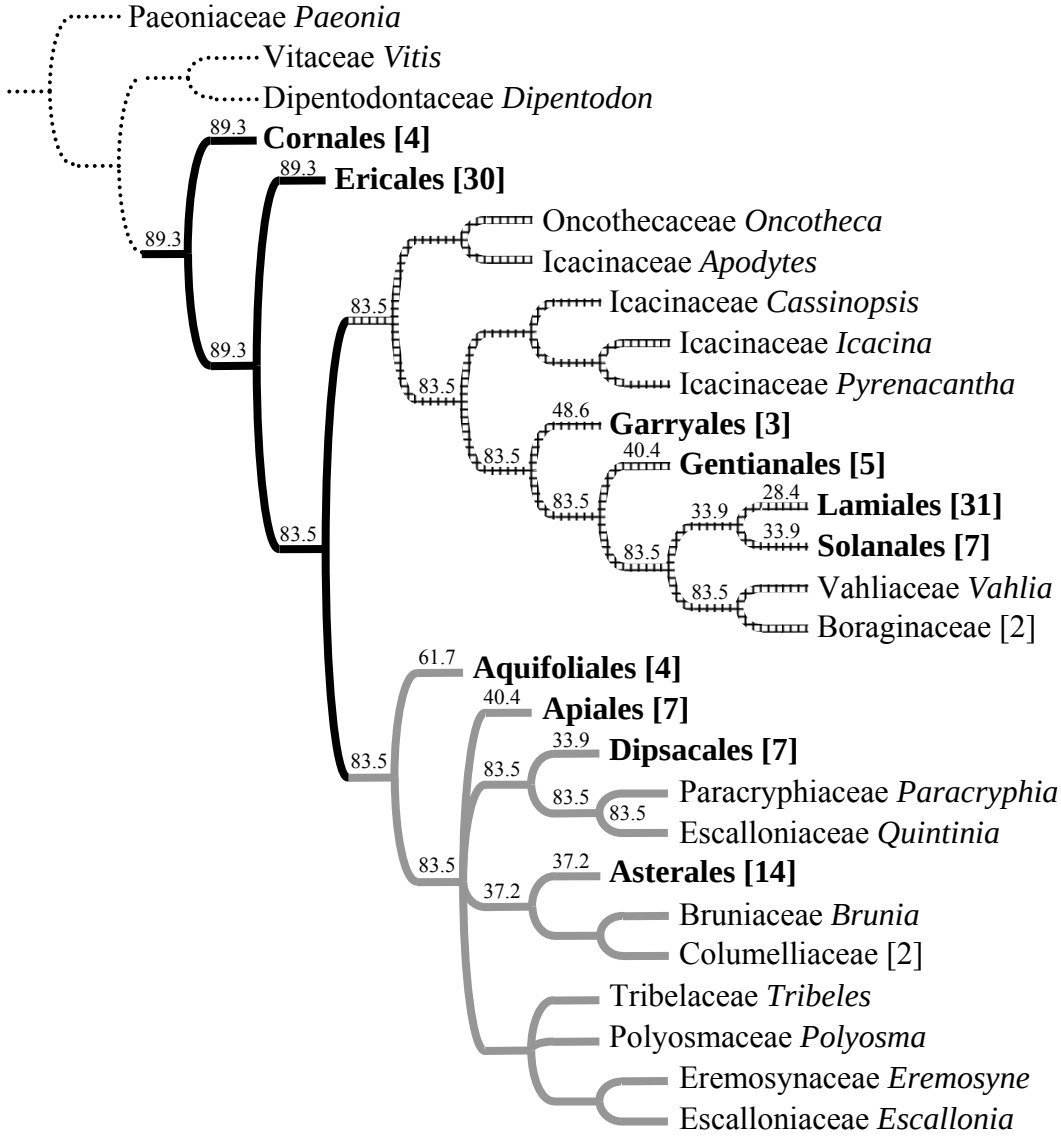


Figure 1.15. Minimum age dating of the Asteridae. Numbers on branches indicate age of the node they precede in millions of years. Cladogram based on Bremer et al. (2002), see Figure 1.1 for explanation of color codes. See Figures 1.2 to 1.14 for sources of minimum ages for each Order and the clade Boraginaceae-Vahliaceae.

DISCUSSION

Interest in establishing ages of origin and diversification of existing taxonomic groups has increased in recent years. Traditionally it has been up to the paleontologists to establish those dates, based on the first appearances of a taxon in the fossil record. Today, with the increase in use in one form or other of molecular clocks, the demand for reliable calibration points has increased accordingly. Now, it is demanded of paleontology that it delivers taxonomically and stratigraphically reliable fossil identifications that can withstand the test of phylogenetic methods (Benton and Donoghue, 2007; Donoghue and Benton, 2007). Phylogenetic methods have provided a means to more stringently test the placement of fossils by identifying synapomorphies that define those groups. Only fossils whose characters have been properly described and compared can be considered confidently identified. Thus only such fossils can be reasonably used in various methods of dating first appearances of taxa.

The survey and evaluation of the early fossil record of the Asteridae carried out in this work (Tables 1.3-1.14) attempts to provide a list of those fossil taxa that have been described as asterids and their degree of reliability. Those fossils that have been included in phylogenetic analyses offer the highest degree of confidence as their characters have been objectively tested against those of assumed related taxa. Unfortunately, very few fossils putatively representing asterids meet this criterion. The fusainized flowers from New Jersey (Nixon and Crepet, 1993; Gandolfo et al., 1998; Martínez-Millán et al., 2009) and Georgia (Keller et al., 1996), the mastixioids reviewed by Tiffney and Haggard (1996), and the fusainized flowers from Sweden analyzed in this work are among the few that have been put to, and passed the test of

the phylogenetic analysis. One of the reasons for the paucity of reliably identified asterids is the lack of available matrices of morphological characters. Since most phylogenetic studies are based on genes, the morphological matrix in which a fossil could be included is rarely compiled.

Two alternative methods for the inclusion of fossil taxa have been proposed; the total evidence analysis and the molecular scaffold approach (Hermsen and Hendricks, 2008). In the total evidence approach, the molecular data and the morphology data are analyzed simultaneously and the fossil taxon is treated as no different as any other terminal in the analysis; the fossil is part of the process of formulating the phylogeny itself. This approach provides the most rigorous test of the relationships of the fossil to the rest of the taxa. The molecular scaffold approach involves finding the most suitable place for the fossil taxa given a pre-defined phylogeny of extant taxa. The fossil is not included in the original analysis that produced the phylogeny, but in a subsequent analysis whose objective is to find the best place for said fossil in that particular phylogeny. This was the approach used in this work to place the fossils *Silvianthemum* and *Scandianthus*. Of the two alternatives, however, the total evidence approach is certainly superior; it increases taxon sampling, increases the amount of information used to create the phylogeny, allows the fossil to impact the phylogenetic hypothesis and allows the discovery of secondary signals (see Hermsen and Hendricks [2008] for a detailed discussion).

A less preferable but still acceptable alternative to the inclusion of the fossil in a phylogenetic analysis, is a description of the fossil with a thorough discussion of diagnostic characters including potential synapomorphies that relate the fossil to a particular clade. About two-thirds of the asterid fossils listed here (175 out of 261)

include such a discussion, which allows the placement of the fossils in the most "suitable" position in the tree according to their characters. The rest of the fossils need to be reevaluated as their descriptions are not detailed and specific enough to be convincing.

It was by following these criteria that the minimum age dating of the Asteridae depicted in Figure 1.15 has been obtained. According to these results, it seems that there have been three diversification "explosions" in the history of the Asteridae marked by the simultaneous first appearances of clades in the fossil record. The first one was in the Late Cretaceous when the four main groups of the Asteridae enter the fossil record; two in the Turonian (89.3 mya) the Cornales and the Ericales, and two in the Santonian (83.5 mya) the Lamiids and the Campanulids. The second one was in the Early Tertiary, around the Eocene (55-33.9 mya) involving most of the euasterid orders. And the third one taking place around the Oligocene when the last order, the Lamiales, diversified (Table 1.15, Figure 1.15).

The fact that more than one fossil places a clade in a particular time frame increases confidence in the reliability of the minimum age of that clade. For example, the minimum age of Late Cretaceous for the Cornales is given by *Tylerianthus crossmanensis* from the Turonian of New Jersey (Table 1.3, Figure 1.2), but if this fossil were to be removed, *Hironoia fusiformis* from Early Coniacian-Early Santonian of Japan would still place the Cornales in the Late Cretaceous (Table 1.3). Even more dramatic is the case of the Ericales as this clade has numerous fossils in the Late Cretaceous (Table 1.4, Figure 1.3). The fact that the fossils come from different geographical locations adds another layer of confidence as the independence across data points (fossil identifications) can be more objectively assessed.

The diversification of the Euasteridae in the Late Cretaceous is, in principle, more difficult to support since there are only three fossils that place this huge clade in the Late Cretaceous: *Scandianthus major*, *Scandianthus costatus* and *Silvianthemum suecicum* (Table 1.12, Figs. 6, 12), and all of them come from the same locality. For this reason, assessing the phylogenetic relationships of these fossils is imperative. In the analyses performed in this work, both fossil taxa were ultimately placed as sisters to the same extant taxa that their authors had suggested based on direct observations: *Silvianthemum* with *Quintinia* and *Scandianthus* with the Vahliaceae (Friis, 1990; Friis and Skarby, 1982). However, these results should be taken with caution. For example, the matrix for the analysis of *Scandianthus* was derived from the same table that the authors built to support their conclusions, therefore, it is not surprising that *Scandianthus* was placed with the Vahliaceae. Independent confirmation of the placement of these fossils, or discovery of other euasterid fossils in the Late Cretaceous would certainly increase confidence in and robustness of these results.

In contrast to the minimum ages obtained from looking at the fossil record, the estimates based on molecular evidence suggest that the diversification of the Asteridae happened during the Early Cretaceous instead of the Late Cretaceous (Table 1.15). However, different molecular dating studies disagree with each other as much as they disagree with the fossil record (Table 1.15).

One of the most frequently cited molecular dating works is that of Wikström et al. (2001) who used non-parametric rate smoothing (NPRS; Sanderson, 1997) and a single calibration point –in the Rosid clade– to date the cladogram of Soltis et al. (2000). In their results, the Asteridae was estimated to have originated 112-122 mya and its diversification to have started some 106-114 mya (Table 1.15). Bremer et al.

(2004), on the other hand, used the cladogram of Bremer et al. (2002) to explicitly estimate the time of origin and divergence of different groups of asterids based on molecular dating (Table 1.15). Three methods were applied: strict molecular clock of Langley and Fitch (1974), non-parametric rate smoothing (NPRS) of Sanderson (1997) and penalized likelihood (PL) of Sanderson (2002), although the authors only report the ages obtained with PL.

A comparison between these ages and the ones estimated by Wikström et al. (2001) indicates that Bremer et al. (2004) consistently got older age estimates than Wikström et al. (2001), between 11 and 30 my older (i.e. Campanulids and Lamiales, Table 1.15). This discrepancy could be due to a number of factors including different methodological tools used for estimating ages (NPRS vs. PL), different phylogenetic hypothesis used (Soltis et al. [2000] vs. Bremer et al. [2002]) and different placement calibration points (one fixed calibration point in the Rosid clade vs. one fixed calibration point at the base of the Asterid clade). However, both molecular-based estimates agree in that they give significantly older estimates than those based on the fossil record alone (Table 1.15).

Advances and improvements in the methods to estimate molecular ages and phylogenies are constantly being produced (see Magallón [2004], Pulquério and Nichols [2007], Soltis et al. [2007]). This will undoubtedly improve our estimates of divergence events, and with it our understanding of evolutionary events in the history of clades. However, even the most precise of methods will deliver unreliable results if the data analyzed are not of good quality, including the fossils used as calibration points. One important step towards the improvement of quality of this calibration points is distinguishing those fossils that can be trusted in their taxonomic assignment

from those that need to be restudied. This work provides that first step for the early fossil record of the Asteridae.

APPENDIX A

CIRCUMSCRIPTION OF THE ASTERIDS

Table 1.16. Circumscription of the asterids under three classification systems. Placement of families that today are considered to be asterids are also given.

Table 1.16. (Continued).

Cronquist (1981)	Takhtajan (1997)		APG (1998, 2003)
Subclass Asteridae	**Subclass Asteridae**		**Asterids**
Order Gentianales	Superorder Campanulanae		Order Cornales
Loganiaceae	Order Campanulales	Order Goodeniales	Curtisiaceae
Retziaceae	Pentaphragmataceae	Brunoniaceae	Grubbiaceae
Gentianaceae	Sphenocleaceae	Goodeniaceae	Hydrangeaceae
Saccifoliaceae	Campanulaceae	Order Stylidiales	Hydrostachyaceae
Apocynaceae	Cyphocarpaceae	Donatiaceae	Loasaceae
Asclepiadaceae	Nemacladaceae	Stylidiaceae	Order Ericales
Order Solanales	Cyphiaceae	Order Menyanthales	Actinidiaceae
Duckeodendraceae	Lobeliaceae	Menyanthaceae	Balsaminaceae
Nolanaceae	Superorder Asteranae		Clethraceae
Solanaceae	Order Calycerales	Order Asterales	Cyrilliaceae
Convolvulaceae	Calyceraceae	Asteraceae	Diapensiaceae
Cuscutaceae	**Subclass Lamiidae**		Ebenaceae
Menyanthaceae	Superorder Gentiananae		Ericaceae
Polemoniaceae	Order Gentianales	Plocospermataceae	Fouqueriaceae
Hydrophyllaceae	Gentianaceae	Order Rubiales	Lecythidaceae
Order Lamiales	Gelsemiaceae	Dialypetalanthaceae	Maesaceae
Lennoaceae	Loganiaceae	Rubiaceae	Marcgraviaceae
Boraginaceae	Strychnaceae	Theligonaceae	Myrsinaceae
Verbenaceae	Antoniaceae	Carlemanniaceae	Pentaphylacaceae
Lamiaceae	Spigeliaceae	Order Apocynales	Polemoniaceae
Order Callitrichales	Saccifoliaceae	Apocynaceae	Primulaceae
Hippuridaceae	Geniostomaceae		Roridulaceae
Callitrichaceae	Superorder Solananae		Sapotaceae
Hydrostachyaceae	Order Solanales	Cuscutaceae	Sarraceniaceae
Order Plantaginales	Solanaceae	Order Boraginales	Styracaceae
Plantaginaceae	Sclerophylacaceae	Boraginaceae	Symplocaceae
Order Scrophulariales	Duckeodendraceae	Hydrophyllaceae	Tetrameristaceae
Buddlejaceae	Goetzeaceae	Tetrachondraceae	Theaceae
Oleaceae	Order Polemoniales	Hoplestigmataceae	Teophrastaceae
Scrophulariaceae	Polemoniaceae	Lennoaceae	Euasterids I
Globulariaceae	Order Convolvulales	Order Limnanthales	Boraginaceae
Orobanchaceae	Convolvulaceae	Limnanthaceae	Icacinaceae

Table 1.16. (Continued).

Cronquist (1981)	Takhtajan (1997)		APG (1998, 2003)
Gesneriaceae	Superorder Loasanae		Oncothecaceae
Acanthaceae	Order Loasales		Vahliaceae
Pedaliaceae	Loasaceae		Order Garryales
Bignoniaceae	Superorder Oleanae		Eucommiaceae
Mendonciaceae	Order Oleales		Garryaceae
Myoporaceae	Oleaceae		Order Gentianales
Lentibulariaceae	Superorder Lamianae		Apocynaceae
Order Campanulales	Order Scrophulariales	Lentibulariaceae	Gelsemiaceae
Pentaphragmataceae	Scrophulariaceae	Order Lamiales	Gentianaceae
Sphenocleaceae	Buddlejaceae	Verbenaceae	Loganiaceae
Campanulaceae	Retziaceae	Lamiaceae	Rubiaceae
Stylidiaceae	Stilbaceae	Phrymaceae	Order Lamiales
Donatiaceae	Oftiaceae	Cyclochilaceae	Acanthaceae
Brunoniaceae	Globulariaceae	Avicenniaceae	Bignoniaceae
Goodeniaceae	Gesneriaceae	Symphoremataceae	Byblidaceae
Order Rubiales	Plantaginaceae	Viticaceae	Calceolariaceae
Rubiaceae	Bignoniaceae	Order Callitrichales	Carlemanniaceae
Theligonaceae	Pedaliaceae	Callitrichaceae	Gesneriaceae
Order Dipsacales	Martyniaceae	Order Hydrostachyales	Lamiaceae
Caprifoliaceae	Trapellaceae	Hydrostrachyaceae	Lentibulariaceae
Adoxaceae	Myoporaceae	Order Hippuridales	Martyniaceae
Valerianaceae	Acanthaceae	Hippuridaceae	Oleaceae
Dipsacaceae	**Subclass Cornidae**		Orobanchaceae
Order Calycerales	Superorder Cornanae		Pawloniaceae
Calyceraceae	Order Hydrangeales	Order Cornales	Pedaliaceae
Order Asterales	Hydrangeaceae	Davidiaceae	Phrymaceae
Asteraceae	Escalloniaceae	Nyssaceae	Plantaginaceae
	Abrophyllaceae	Mastixiaceae	Plocospermataceae
	Argophyllaceae	Curtisiaceae	Schlegeliaceae
in APG's Asteridae	Corokiaceae	Cornaceae	Scrophulariaceae
Subclass Dillenidae	Alseuosmiaceae	Alangiaceae	Stilbaceae
Order Theales	Carpodetaceae	Order Garryales	Tetrachondraceae
Theaceae	Phyllonomaceae	Garryaceae	Verbenaceae
Actinidiaceae	Pottingeriaceae	Order Aucubales	Order Solanales
Pentaphylacaceae	Tribelaceae	Aucubaceae	Convolvulaceae
Scytopetalaceae	Melanophyllaceae	Order Griseliniales	Hydroleaceae
Pellicieraceae	Montiniaceae	Griseliniaceae	Montiniaceae
Tetrameristaceae	Kaliphoraceae	Order Eucommiales	Solanaceae
Oncothecaceae	Columelliaceae	Eucommiaceae	Sphenocleaceae
Marcgraviaceae	Order Desfontainiales	Order Aralidiales	Euasterids II
Paracryphiaceae	Desfontainiaceae	Aralidiaceae	Bruniaceae
Order Lecythidales	Order Roridulales	Order Torriceliales	Columelliaceae
Lecythidaceae	Roridulaceae	Torriceliaceae	Eremosynaceae

Table 1.16. (Continued).

Cronquist (1981)	Takhtajan (1997)		APG (1998, 2003)
Order Nepenthales	Superorder Aralianae		Escalloniaceae
Sarraceniaceae	Order Helwingiales	Apiaceae	Paracryphiaceae
Order Violales	Helwingiaceae	Order Pittosporales	Polyosmaceae
Fouqueriaceae	Order Araliales	Pittosporaceae	Sphenostemonaceae
Loasaceae	Araliaceae	Order Byblidales	Tribelaceae
Order Ericales	Hydrocotylaceae	Byblidaceae	Order Apiales
Cyrillaceae	Superorder Dipsacanae		Apiaceae
Clethraceae	Order Dipsacales	Order Viburnales	Araliaceae
Grubbiaceae	Caprifoliaceae	Viburnaceae	Aralidiaceae
Ericaceae	Valerianaceae	Order Adoxales	Griseliniaceae
Pyrolaceae	Triplostegiaceae	Adoxaceae	Mackinlayaceae
Monotropaceae	Dipsacaceae	Sambucaceae	Melanophyllaceae
Empetraceae	Morinaceae		Myodocarpaceae
Epacridaceae			Pennatiaceae
Order Diapensales			Pittosporaceae
Diapensiaceae	***in APG's Asteridae***		Torricelliaceae
Order Ebenales	**Subclass Dillenidae**		Order Aquifoliales
Ebenaceae	Superorder Theanae		Aquifoliaceae
Sapotaceae	Order Paracryphiales	Order Theales	Cardiopteridaceae
Styracaceae	Paracryphiaceae	Theaceae	Helwingiaceae
Symplocaceae	Order Lecythidales	Pentaphylacaceae	Phyllonomaceae
Lissocarpaceae	Lecythidaceae	Tetrameristaceae	Stemonuraceae
Order Primulales	Barringtoniaceae	Oncothecaceae	Order Asterales
Theophrastaceae	Napoleonaeaceae	Marcgraviaceae	Alseuosmiaceae
Myrsinaceae	Foetidiaceae	Pellicieraceae	Argophyllaceae
Primulaceae	Asteranthaceae		Asteraceae
Subclass Rosidae	Superorder Sarracenianae		Calyceraceae
Order Rosales	Order Sarraceniales		Campanulaceae
Pittosporaceae	Sarraceniaceae		Goodeniaceae
Byblidaceae	Superorder Ericanae		Menyanthaceae
Hydrangeaceae	Order Ericales	Order Diapensales	Pentaphragmataceae
Columelliaceae	Ericaceae	Diapensiaceae	Phellinaceae
Bruniaceae	Clethraceae	Order Bruniales	Rousseaceae
Alseuosmiaceae	Cyrillaceae	Bruniaceae	Stylidiaceae
Order Cornales	Epacridaceae	Grubbiaceae	Order Dipsacales
Cornaceae	Empetraceae		Adoxaceae
Alangiaceae	Superorder Primulanae		Caprifoliaceae
Nyssaceae	Order Primulales	Lissocarpaceae	Diervillaceae
Garryaceae	Primulaceae	Order Sapotales	Dipsacaceae
Order Celastrales	Order Styracales	Sapotaceae	Linnaeaceae
Aquifoliaceae	Styracaceae	Order Myrsinales	Morinaceae
Icacinaceae	Symplocaceae	Myrsinaceae	Valerianaceae
Cardiopteridaceae	Ebenaceae	Theophrastaceae	

Table 1.16. (Continued).

Cronquist (1981)	Takhtajan (1997)	APG (1998, 2003)
Order Geraniales	**Subclass Rosidae**	
Balsaminaceae	Superorder Saxifraganae	
Order Apiales	Order Saxifragales	
Apiaceae	Eremosynaceae Vahliaceae	
Araliaceae	Superorder Geranianae	
	Order Balsaminales	
	Balsaminaceae	
	Superorder Celastranae	
	Order Brexiales Phellinaceae	
	Rousseaceae Sphenostemonaceae	
	Order Icacinales Order Cardiopteridales	
	Icacinaceae Cardiopteridaceae	
	Aquifoliaceae	

APPENDIX B

PHYLOGENETIC ANALYSIS OF *SILVIANTHEMUM* FRIIS 1990

Although the fossil taxon *Silvianthemum suecicum* Friis 1990 was included in a phylogenetic analysis (Backlund [1996] using the Backlund and Donoghue [1996] matrix of morphological characters), it is appropriate to revisit this taxon as the aforementioned analysis is not compatible with more recent and robust hypotheses of phylogenetic relationships. For this new analysis, characters 32-60 -representing floral morphology, androecium, gynoecium and fruit characters– of the Backlund and Donoghue (1996) matrix of morphological characters were used. *Silvianthemum* was coded based on its original description (Friis, 1990). The resulting matrix has 59 taxa, including the fossil taxon and 29 characters (Table 1.17):

32. Sexual distribution: bisexual = 0; dioecious = 1; gynodioecious = 2; trioecious = 3.
33. Perianth position: hypogynous = 0; semi-epigynous = 1; epigynous = 2.
34. Flower/corolla orientation: one petal adaxial = 0; one petal abaxial = 1.
35. Sepal size: absent or not visible = 0; very reduced, inrolled plumes or minute teeth = 1; well developed prominent = 2.
36. Sepals, number of: 2 = 0; 3 = 1; 4 = 2; 5 = 3; 6 or more, indefinite = 4.
37. Sepal vascularization: 1 trace = 0; 3 traces = 1; 4 traces = 2; 5 traces = 3.
38. Sepal modification for fruit dispersal: none = 0; developing into a plumose seed/ fruit = 1; developing to seeds/fruits with awns/bristles = 2; enlarged and leaflike aiming for wind dispersal = 3.
39. Petal and sepal folding-pattern in buds: valvate = 0; imbricate = 1.
40. Petal fusion: fused = 0; free = 1.

41. Petals, number of: 3 petals/lobes = 0; 4 petals/lobes = 1; 5 petals/lobes = 2; 6 or more petals/lobes = 3; unnamed state = 4 [sic].
42. Corolla tube: petals weakly connate or no tube = 0; tube rotate/small but distinct = 1; tube well developed/long = 2.
43. Corolla symmetry: actinomorphic = 0; weakly zygomorphic = 1; strongly zygomorphic/bilabiate = 2.
44. Corolla nectary type: absent = 0; nectar disk = 1; multicellular hairs = 2; unicellular hairs = 3.
45. Corolla nectary number: 1, or fewer than number of lobes = 0; 1-5, or equal to number of lobes = 1.
46. Corolla vascularization: lacking lateral connections = 0; with lateral connections = 1.
47. Stamen number: 1 = 1; 2 = 2; 3 = 3; 4 = 4; 5 = 5; 6-more, indefinite = 6.
48. Stamen relative length: equal in length = 0; prominently unequal in length = 1; didynamous = 2.
49. Staminal filament indumentum: glabrous = 0; hairy = 1; unnamed state = 2.
50. Filament attachment: free from corolla = 0; weakly fused to corolla = 1; prominently fused to corolla = 2.
51. Staminal modifications: all stamens fertile = 0; sterile staminodia present = 1.
52. Anther attachment: dorsifixed = 0; basifixed = 1; sagittate = 2.
53. Anther orientation at dehiscence: extrorse = 0; introrse = 1.
54. Sporangium number in thecae: 1 = 0; 2 = 1.
55. Carpels, number: 1 = 1; 2 = 2; 3 = 3; 4 = 4; 5 = 5.
56. Carpel abortion: all fertile = 0; one aborted = 1; two adjacent aborted = 2; two adjacent aborted and ovule displaced = 3; two opposite aborted = 4.

57. Sterile loci: none = 0; present but much reduced and visible only as minor openings = 1; normal/prominent in cross sectioning of ovary = 2.

58. Carpel vascularization: free adaxial and abaxial = 0; adaxial bundles only = 1; only free abaxial, adaxial not recessed = 2.

59. Stigma shape: entire and slender = 0; capitate = 1; bilobate = 2; trilobate = 3; pentalobate = 4.

60. Fruit type: capsule loculicidal = 0; capsule septicidal = 1; berry = 2; drupe = 3; cypsela, with persistent remains of calyx = 4; cypsela, lacking remains of calyx = 5; schizocarp = 6.

Table 1.17. Characters 32 to 60 of the Backlund and Donoghue (1996) matrix of morphological characters with *Silvianthemum suecicum* Friis 1990.

Taxa/characters	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Silvianthemum	0	2	?	1	3	-	-	1	1	2	0	0	1	0	-	6	0	0	0	0	0	?	1	3	0	0	?	1	?
Adoxa	0	1	0	2	12	0	0	1	0	12	1	01	2	1	01	45	0	0	1	0	0	0	1	45	0	0	0	1	3
Sinadoxa	0	1	0	2	012	0	0	1	0	01	1	1	2	1	0	34	0	0	1	0	0	0	1	4	0	0	?	0	?
Tetradoxa	0	01	0	2	2	0	0	1	0	1	1	0	2	1	01	4	0	0	1	0	0	0	1	4	0	0	?	1	?
Abelia	0	2	1	2	3	1	3	1	0	2	2	12	3	0	1	4	2	1	2	0	2	1	1	3	2	0	2	1	4
Diervilla	0	2	1	2	3	01	0	1	0	2	2	12	3	0	1	5	0	1	2	0	2	1	1	2	0	0	2	1	1
Dipelta	0	2	1	2	3	1	0	1	0	2	2	12	3	0	1	4	2	1	2	0	02	1	1	4	2	0	2	1	4
Heptacodium	0	2	1	2	3	1	0	1	0	2	2	12	3	0	1	5	0	0	2	0	0	1	1	3	2	2	2	1	3
Kolkwitzia	0	2	1	2	3	1	0	1	0	2	2	2	3	0	1	4	2	1	2	0	2	1	1	3	2	12	2	1	4
Leycesteria	0	2	1	2	3	1	0	1	0	2	2	01	3	1	1	5	0	01	2	0	2	1	1	45	0	0	2	1	2
Linnaea	0	2	1	2	3	1	0	1	0	2	2	1	3	0	1	4	2	0	2	0	2	1	1	3	2	0	2	1	4
Lonicera	0	2	1	2	3	1	0	1	0	2	2	012	3	1	1	5	0	101	2	0	2	1	1	23	0	0	2	1	2
Symphoricarpos	0	2	1	2	3	1	0	1	0	12	2	01	3	0	1	45	0	0	2	0	2	1	1	4	4	0	2	1	3
Triosteum	0	2	1	2	3	1	0	1	0	2	2	2	3	0	1	5	0	1	2	0	2	1	1	4	1	0	2	1	3
Weigela	0	2	1	2	3	1	0	1	0	2	2	12	3	0	1	5	0	01	2	0	2	1	1	2	0	0	2	1	1
Zabelia	0	2	1	2	23	01	3	1	0	12	2	12	3	0	1	45	2	1	2	0	2	1	1	3	2	0	2	1	4
Dipsacus	0	2	1	1	4	2	2	1	0	1	2	2	3	0	1	4	0	2	2	0	0	1	1	3	2	01	2	01	6
Knautia	01	2	1	1	24	1	2	1	0	1	2	2	3	0	1	4	0	1	2	0	0	1	1	3	2	01	2	23	5
Pterocephalus	0	2	1	12	24	2	1	1	0	12	2	12	3	0	1	4	0	2	2	0	0	1	1	3	2	01	2	1	4
Scabiosa	0	2	1	1	3	1	2	1	0	2	2	2	3	0	1	4	0	2	2	0	0	1	1	3	2	01	2	2	4
Succisa	0	2	1	1	23	12	2	1	0	1	2	1	3	0	1	4	0	2	2	0	0	1	1	3	2	01	2	12	4
Acanthocalyx	0	2	1	2	2	1	0	1	0	2	2	2	3	0	1	4	2	2	2	0	0	1	1	3	2	1	2	1	4
Cryptothladia	0	2	1	2	2	1	0	1	0	2	2	2	3	0	1	4	2	01	2	1	0	1	1	3	2	1	2	1	4
Morina	0	2	1	2	2	2	0	1	0	2	2	2	3	0	1	4	2	01	2	1	0	0	1	3	2	1	2	1	4

Table 1.17. (Continued).

Taxa/characters	32	3334	35	36	37383940	41	42	43	444546	47	48495051525354	55	565758	59	60
Sambucus	0	12 1	1	123	0 0 01 0	012	1	0	1 0 1	345	0 0 1 0 1 1 1	345	0 0 0	34	3
Triplostegia	0	2 1	1	2	0 0 1 0	2	2	1	3 0 1	4	0 0 2 0 0 1 1	3	2 1 2	1	4
Belonanthus	23	2 1	1	1	1 0 1 0	0	2	1	3 0 1	3	0 0 2 0 1 1 0	3	2 01 1	23	4
Centranthus	0	2 1	1	3	0 1 1 0	2	2	2	3 0 1	1	0 0 2 0 0 1 1	3	2 01 2	13	4
Nardostachys	0	2 1	2	3	1 3 1 0	2	2	1	3 0 1	145	0 0 2 0 0 1 1	3	2 2 2	1	4
Patrinia	0	2 1	01	3	0 03 1 0	2	2	1	3 0 1	145	0 0 2 0 0 1 1	3	2 2 2	1	4
Phyllactis	0123	2 1	0	0	0 0 1 0	012	2	12	0 0 1	3	0 0 2 0 0 1 0	3	2 01 2	3	5
Plectritis	0	2 1	1	3	0 0 1 0	2	2	2	3 0 1	3	1 0 2 0 0 1 1	3	2 12 2	23	5
Stangea	0	2 1	1	4	0 1 1 0	2	2	1	3 0 01	3	0 0 2 0 01 1 0	3	2 01 2	2	4
*V_clematitis**	2	2 1	1	4	0 1 1 0	2	2	1	3 0 1	3	0 0 2 0 1 1 1	3	2 1 2	3	4
*V_dioica**	1	2 1	1	4	0 1 1 0	2	2	1	3 0 1	3	0 0 2 0 0 1 1	3	2 1 2	2	4
*V_hirtella**	0	2 1	1	4	0 1 1 0	2	2	1	3 0 1	3	0 0 2 0 1 1 1	3	2 1 2	3	4
*V_officinalis**	0	2 1	1	3	0 1 1 0	2	2	1	3 0 1	3	0 0 2 0 0 1 1	3	2 0 2	3	4
Valerianella	0	2 1	2	3	0 0 1 0	2	2	12	3 0 0	3	0 0 2 0 0 1 1	3	2 2 2	3	5
Viburnum	01	1 1	1	3	0 0 1 0	2	12	0	1 0 0	5	02 0 12 0 1 1 1	3	3 1 0	3	3
Apium	0	2 0	012	3	0 0 0 1	2	0	01	1 0 0	5	0 0 0 0 1 1 1	2	0 0 0	2	6
Staganotaenia	0	2 0	2	3	0 0 0 1	2	0	0	1 0 0	5	0 0 0 0 1 1 1	2	0 0 0	2	6
Aralia	01	2 01	1	23	0 0 1 01	12	0	0	1 0 0	5	0 0 0 0 1 1 1	2345	0 2 0	0	23
Aralidium	1	2 1	1	3	0 0 1 0	2	0	0	1 0 0	5	0 0 0 0 0 1 1	3	2 0 0	3	3
Audouinia	0	1 1	2	3	0 0 1 1	2	0	0	1 0 0	5	0 0 0 0 2 1 1	3	2 2 0	3	0
Berzelia	0	1 1	2	3	0 0 1 1	2	0	0	0 0 0	5	0 0 0 0 2 0 1	1	0 0 2	0	5
Brunia	0	1 1	2	3	0 0 1 1	2	0	0	0 0 0	5	1 0 0 0 2 0 1	12	0102 2	0	45
Columellia	0	1 1	2	3	0 0 1 0	2	2	1	1 0 0	5	0 0 2 0 1 0 1	2	0 0 0	2	1
Desfontainia	0	0 1	2	3	1 0 1 0	2	2	1	1 0 1	5	0 0 2 0 1 1 1	5	0 0 0	12	2
Eremosyne	02	1 0	2	3	0 0 0 1	2	0	0	1 0 0	5	0 0 0 0 0 1 1	2	0 0 ?	1	0
Anopterus	0	0 0	2	4	1 0 1 1	4	0	0	0 ? 0	5	0 0 0 0 2 1 1	2	0 0 2	0	1
Escallonia	0	1 0	2	3	13 0 0 01	2	012	0	1 0 0	5	0 0 0 0 0 1 1	2	0 01021	234	1
Forgesia	0	1 0	2	3	0 0 0 1	2	0	0	1 0 0	5	0 1 0 0 2 1 1	2	0 0 0	1	1
Quintinia	0	1 0	2	3	0 0 1 1	2	0	0	1 0 0	5	0 0 0 0 0 1 1	345	0 0 0	0	1
Griselinia	1	2 ?	01	3	? 0 1 1	2	0	0	1 0 0	5	0 0 0 0 0 1 1	3	2 01 2	3	3
Melanophylla	0	2 1	2	3	0 0 1 1	2	0	0	1 0 0	5	0 0 0 0 2 1 1	23	01 0 2	0	3
Pittosporum	01	0 1	2	3	0 0 1 01	2	012	0	0 0 0	5	0 0 2 0 1 1 1	2	0 0 0	02	0
Polyosma	0	2 ?	2	2	13 0 0 1	1	2	0	1 0 0	4	0 1 0 0 1 1 1	1	0 0 0	1	2
Torricellia	1	2 1	2	3	0 0 0 1	2	0	0	1 0 0	5	0 0 0 0 1 1 1	3	2 2 ?	3	3
Tribeles	0	0 ?	2	3	0 0 1 1	2	0	0	1 0 0	5	0 0 0 0 1 1 1	3	0 0 2	3	1

**Valeriana*

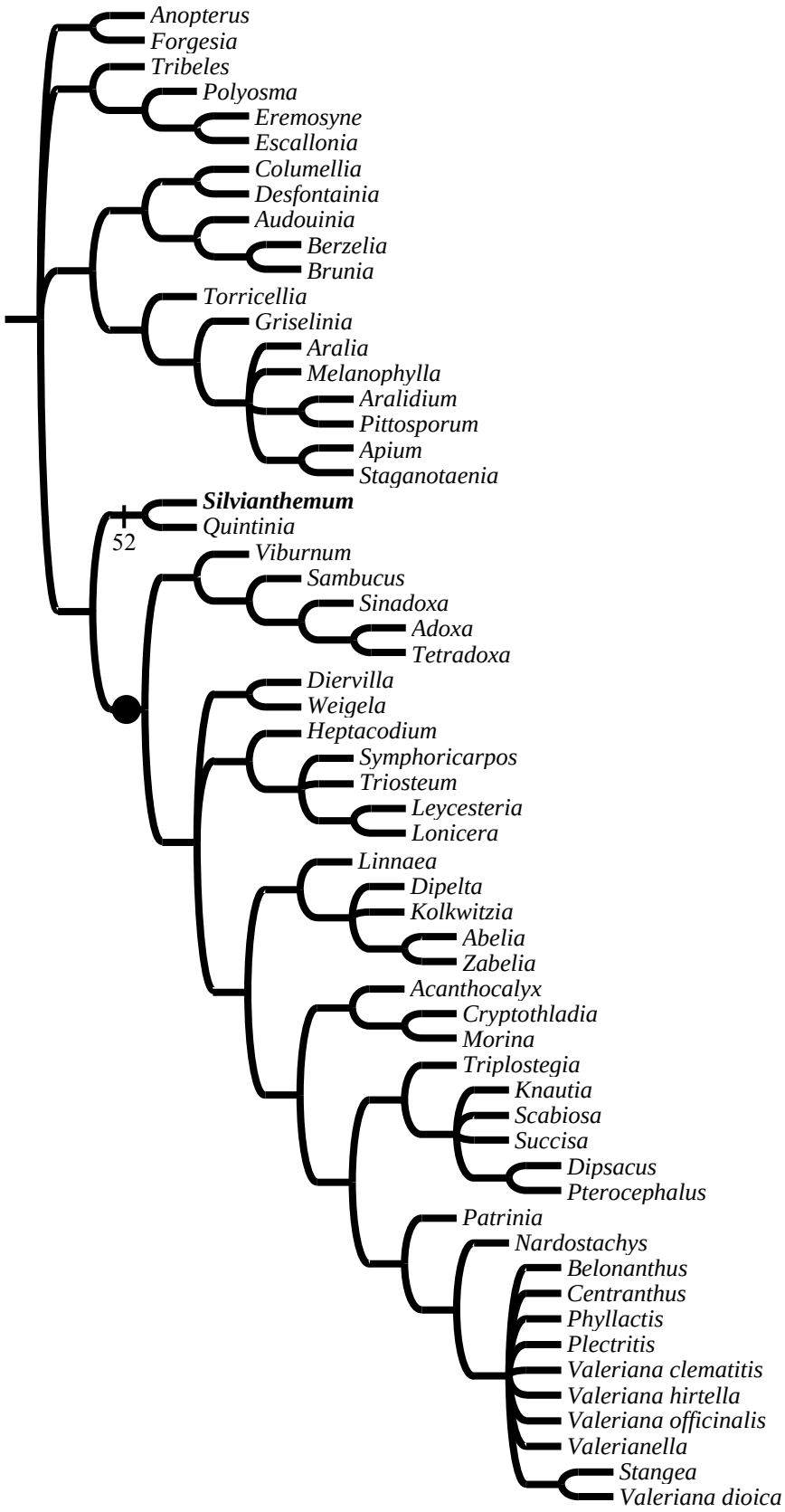
The analysis of Bremer et al. (2002) showed that the Escalloniaceae is a polyphyletic group and that part of it, namely *Quintinia* is more closely related to the Dipsacales than to the rest of the family. It also showed that the Columelliaceae and the Bruniaceae do not belong with the Dipsacales and that *Polyosma* and *Tribeles* do not belong with the Apiales. These results differ enough from Backlund and Donoghue (1996) that a reevaluation of the position of *Silvianthemum* is justified.

In this work, the 59 extant taxa used by Backlund and Donoghue (1996) were rearranged in clades following the results of Bremer et al. (2002), Donoghue et al. (2003) and Zhang et al. (2003). The backbone tree and its group membership matrix were constructed in Winclada version 1.00.08 (Nixon, 2002). In order to allow *Silvianthemum* to "float" free among all possible positions in the cladograms, all its cells were changed to "?". Similarly, those taxa not included in the Bremer et al. (2002), Donoghue et al. (2003) or Zhang et al. (2003) works –*Zabelia*, *Knautia*, *Succisa*, *Belonanthus*, *Phyllactis* and *Stangea*– were allowed to "float" free inside the Dipsacales clade by changing their scores to "?" in all characters that defined relationships within that clade. All characters were assigned a weight of 50.

The group membership matrix and the matrix of morphological characters matrix were combined in Winclada. A total of 10 heuristic searches were run in NONA version 2.0 (Goloboff, 1999) where each run consisted on 1000 replications of SPR searches on randomly generated initial wagner trees, holding up to 10 trees per replication with an additional TBR on the resulting trees (>h10001; rs0; h/10; mult*1000; max*). The resulting trees were combined in Winclada where suboptimal and duplicate trees were eliminated and a strict consensus was calculated.

The analysis yielded 312 trees whose strict consensus was rerooted to match the basal polytomy of the Campanuliid clade showed in Bremer et al. (2002). In this strict consensus (Figure 1.16), *Silvianthemum* and *Quintinia* are sister groups with dorsifixed anther attachment as synapomorphy (ch 52). The Dipsacales is the sister group of this clade.

Figure 1.16. Strict consensus of 312 trees (L=204, CI=32, RI=68 each) rerooted to match the basal polytomy of the Campanuliid clade found by Bremer et al. (2002). The consensus shows the position of the fossil *Silvianthemum* as sister to *Quintinia* with dorsifixed anther attachment as synapomorphy (ch 52) and the Dipsacales (black circle) as their sister group.


Anopterus
Forgesia
Tribeles
Polyosma
Eremosyne
Escallonia
Columellia
Desfontainia
Audouinia
Berzelia
Brunia
Torricellia
Griselinia
Aralia
Melanophylla
Aralidium
Pittosporum
Apium
Staganotaenia
Silvianthemum
Quintinia
52
Viburnum
Sambucus
Sinadoxa
Adoxa
Tetradoxa
Diervilla
Weigela
Heptacodium
Symphoricarpos
Triosteum
Leycesteria
Lonicera
Linnaea
Dipelta
Kolkwitzia
Abelia
Zabelia
Acanthocalyx
Cryptothladia
Morina
Triplostegia
Knautia
Scabiosa
Succisa
Dipsacus
Pterocephalus
Patrinia
Nardostachys
Belonanthus
Centranthus
Phyllactis
Plectritis
Valeriana clematitis
Valeriana hirtella
Valeriana officinalis
Valerianella
Stangea
Valeriana dioica

APPENDIX C

PHYLOGENETIC ANALYSIS OF *SCANDIANTHUS* FRIIS AND SKARBY 1982

In order to test the assignment of the fossil genus *Scandianthus* to the Vahliaceae in a phylogenetic context, the characters used by the authors in their original description of the fossil taxon were used to create a data matrix. In Friis and Skarby's (1982) original table, *Scandianthus* was compared to 28 families then assigned to the Saxifragales. In the table most columns represent character states (absent/present scoring) and not independent characters, here, this situation was addressed by creating multistate unordered characters. The resulting data matrix has 12 characters (Table 1.18):

1. Flower sex: bisexual = 0; unisexual = 1.
2. Flower part position: epigynous = 0; perigynous = 1; hypogynous = 2.
3. Perianth part connation: floral parts free = 0; floral parts fused = 1.
4. Androecium number: diplostemonous = 0; obdiplostemonous = 1; haplostemonous = 2; numerous stamens = 3.
5. Carpel number: 2 = 0; 3-5(-15) = 1.
6. Apo/Syncarpic gynoecium: apocarpous = 0; syncarpous = 1.
7. Locule number: 1 = 0; 2-5(-15) = 1.
8. Style number in syncarpous gynoecium: 1 = 0; 2 = 1.
9. Capsule as fruit: capsule = 0; other than capsule (berry, drupe or nut) = 1.
10. Placentae pendant: absent = 0; present = 1.
11. Ovule relative number: few = 0; many = 1.
12. Nectary disc: absent = 0; present = 1.

Table 1.18. Data matrix of morphological characters derived from the table presented by Friis and Skarby (1982).

Taxa/Characters	1	2	3	4	5	6	7	8	9	10	11	12
Cunoniaceae	01	2	0	1	01	1	1	0	01	0	1	1
Davidsoniaceae	0	2	1	3	0	1	1	1	1	0	0	1
Eucryphiaceae	0	2	0	3	1	0	-	-	?	0	1	0
Paracryphiaceae	1	2	?	3	1	1	1	?	0	0	0	0
Crypteroniaceae	01	12	01	2	01	1	1	0	0	0	01	0
Brunelliaceae	1	2	01	0	01	0	-	-	?	0	0	1
Escalloniaceae	0	012	01	2	01	1	01	01	01	0	1	1
Tribelaceae	0	2	01	2	1	1	1	?	0	0	1	0
Tetracarpaceae	0	2	01	1	1	0	-	-	?	0	1	0
Iteaceae	0	12	0	2	01	1	1	01	0	0	01	1
Brexiaceae	0	2	01	2	1	1	1	?	01	0	01	1
Phyllonomaceae	0	0	0	2	0	1	01	1	1	0	1	1
Pterostemonaceae	0	0	0	1	1	1	1	?	0	0	0	0
Grossulariaceae	0	0	0	2	0	1	0	1	1	0	1	0
Hydrangeaceae	01	01	01	013	01	1	01	01	0	0	1	1
Montiniaceae	1	0	01	2	0	1	1	0	0	0	0	1
Roridulaceae	0	2	0	2	1	1	1	?	0	0	0	0
Pittosporaceae	01	2	01	2	01	1	01	0	01	0	1	0
Byblidaceae	0	2	01	2	0	1	1	0	0	0	1	0
Bruniaceae	0	2	1	2	?	?	0	?	1	0	0	1
Penthoraceae	0	2	0	1	1	0	-	-	?	0	1	0
Crassulaceae	0	02	0	12	1	0	-	-	?	0	1	0
Cephalotaceae	0	12	0	1	1	0	-	-	?	0	0	1
Saxifragaceae	0	012	0	12	01	1	01	01	01	1	1	0
Vahliaceae	0	0	0	2	0	1	0	1	0	1	1	1
Francoaceae	0	2	01	12	01	1	0	0	0	0	1	0
Eremosynaceae	0	12	01	2	0	1	0	1	0	0	0	0
Parnassiaceae	0	12	0	1	0	1	0	1	0	0	1	0
Scandianthus	0	0	0	0	0	1	0	1	0	1	1	1

The families used by Friis and Skarby (1982) were then thought to form the saxifragalean complex. The phylogenetic analyses by Soltis et al. (2000) dismembered this "saxifragalean complex" by showing that these families are distantly related. The works of Soltis et al. (2000), Bremer et al. (2002) and APG (2003) were used here to create a fixed backbone compatible with these newer hypotheses of relationships. This backbone tree was constructed in Winclada version 1.00.08 (Nixon, 2002) and a group

membership matrix was derived from it. In this matrix (29 taxa, 20 characters) all character states for *Scandianthus* were changed to "?" and all characters were assigned a weight of 20. The group membership matrix and the morphological characters matrix were combined in Winclada and 10 heuristic searches were run in NONA version 2.0 (Goloboff, 1999). Each run consisted on 1000 replications of SPR searches on randomly generated initial wagner trees, holding up to 10 trees per replication with an additional TBR on the resulting trees (>h10001; rs0; h/10; mult*1000; max*). The resulting trees were combined in Winclada where suboptimal and duplicate trees were eliminated and a strict consensus was calculated.

The searches resulted in 32 trees whose strict consensus was rerooted in the node between the Saxifragales and the Rosid-Asterid clade (Figure 1.17). The strict consensus shows *Scandianthus* as sister to Vahliaceae based on both having one locule (ch 7) and pendant placentae (ch 10).

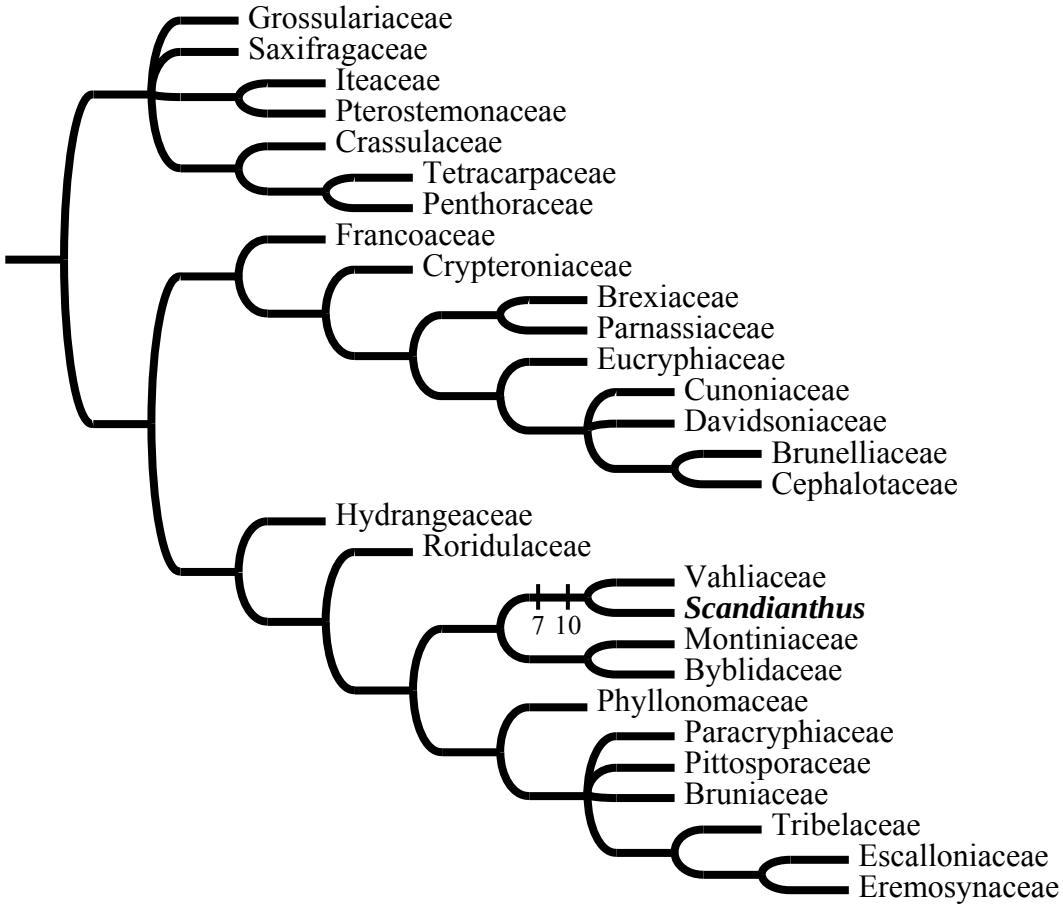


Figure 1.17. Strict consensus of 32 trees (L=62, CI=22, RI=28 each) rerooted in the node between the Saxifragales and the Rosid-Asterid clade. *Scandianthus* was resolved as sister to Vahliaceae based the synapomorphies one locule (ch 7) and pendant placentae (ch 10).

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CHAPTER 2

PENTAPETALUM TRIFASCICULANDRICUS GEN. ET SP. NOV., A THEALEAN FOSSIL FLOWER FROM THE RARITAN FORMATION, NEW JERSEY, USA. (TURONIAN, LATE CRETACEOUS)*

INTRODUCTION

For centuries, the study of the fossil record has been the only way to learn about the life forms that once populated the Earth. Therefore, the fossil record has a double value; it is informative as well as corroborative. It can unveil new and unpredicted ancient life forms as well as give independent support or disprove hypotheses produced by other methods of analysis (Crepet, 2000). For these reasons, it is imperative that the identification of the fossils be accurate, based on strict and objective analysis of their characters, preferably in a phylogenetic context.

In the case of angiosperms, the fossil record shows their sudden appearance in the mid to late Early Cretaceous, some 125 mya (Friis et al., 2001, Sun et al., 2002), followed by a rapid diversification (Crepet, 2000, 2008; Friis et al., 2006) that led to the establishment of most major clades and many modern families by the Late Cretaceous (Crepet et al., 2004). Rich Cretaceous fossil localities, such as those in New Jersey, Georgia, and Sweden, have produced a number of fossil taxa that have reshaped our understanding of Cretaceous floras and of angiosperm diversification.

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The fossil deposits of the Late Cretaceous Old Crossman Clay Pit locality of Sayreville, New Jersey have yielded an abundance of exquisitely preserved fossil plants that span all major lineages of land plants: mosses (Crepet et al., 2001), ferns (Gandolfo et al., 1997, 2000), gymnosperms (Crepet et al., 2001; Gandolfo et al., 2001), and most frequently, angiosperms (Crepet, 1996; Crepet et al., 2001). Among the many angiosperm lineages represented in these sediments are early-diverging groups like Nymphaeaceae (Gandolfo et al., 2004); magnoliids like Calycanthaceae (Crepet et al., 2005), Lauraceae (Herendeen et al., 1994), Chloranthaceae (Herendeen et al., 1993) and Magnoliaceae (Crepet and Nixon, 1994, 1998b); monocotyledons (Gandolfo et al., 2002); rosids like Hamamelidaceae (Crepet et al., 1992; Zhou et al., 2001), Iteaceae (Hermsen et al., 2003), Capparales (Gandolfo et al., 1998a) and Clusiaceae (Crepet and Nixon, 1998a); and asterids, especially Cornales (Gandolfo et al., 1998b) and Ericales (Nixon and Crepet, 1993; Weeks et al., 1996).

Herein, we describe a new taxon with affinities to the Theaceae s.l. The Theaceae have proved to be a challenging group whose circumscription and relationships have been difficult to elucidate (Prince and Parks, 2001; Luna and Ochoterena, 2004; Yang et al., 2004; Wang et al., 2006). Cronquist (1981), based on morphology, placed the Theaceae in the order Theales, class Dillenidae along with families that today are thought to belong in distantly related clades (APG, 1998, 2003). Similarly, Takhtajan (1997) placed the Theaceae in his class Dillenidae, close to families that today are considered to be very distantly related (i.e., his order Hypericales, which follows the order Theales in his classification scheme). Both authors also adopted a broad circumscription of the family that absorbs the Ternstroemiaceae. Currently, based on molecular evidence, the Theaceae s.l. is considered to be nonmonophyletic, with its genera forming two clades, the Theaceae

s.s. (former subfamily Camellioidae; Keng, 1962; Luna and Ochoterena, 2004) and the Ternstroemiaceae (former subfamily Ternstroemioidae; Keng, 1962; Luna and Ochoterena, 2004). The Theaceae is currently placed in the Ericales (Bremer et al., 2002), a complex but well-supported group whose phylogenetic relationships are still not completely resolved (Schönenberger et al., 2005).

Although phylogenetic relationships within Ericales are still being debated, the evidence supports an early diversification of the group: *Paleoenkianthus sayrevillensis*, a flower with derived characters related to the Ericaceae and several undescribed flowers of ericalean affinities (Crepet, 1996; Weeks et al., 1996) date back to the Turonian of New Jersey in North America (Nixon and Crepet, 1993), *Paradinandra suecica* (Schönenberger and Friis, 2001) and *Actinocalyx bohrii* (Friis, 1985), both with a generalized ericalean morphology, date from the Late Santonian-Early Campanian of Sweden, and the actinidiaceous *Parasaurauia allonensis* (Keller et al., 1996) dates from the Early Campanian of Georgia, North America. An early diversification of the group is not only supported by the diverse morphologies found early in the fossil record but also by the geographical extension of these findings; the east coast of North America and northern Europe. The fossil taxon described here further supports this conclusion because it shows new combinations of ericalean characters not seen in any of the other fossils.

MATERIALS AND METHODS

Locality— The fossils were collected at the Old Crossman Clay Pit locality from the South Amboy Fire Clay Member (Fig. 2.1). Traditionally, this member has been considered to be upper Raritan Formation (i.e., Owens and Minard, 1960; Groot et al., 1961; Wolfe and Pakiser, 1971; Doyle and Robbins, 1977; Christopher, 1977,

1979), but according to some authors it might fit better as lower Magothy Formation (Owens et al., 1977; Christopher, 1979; Sugarman et al., 2005). The outcrop belongs to the Atlantic Coastal Plain Geological Province (Fig. 2.1) and is located in Sayreville, Middlesex County, New Jersey, USA, south of the Raritan River, approximately 40º 28' N and 74º 19' W.

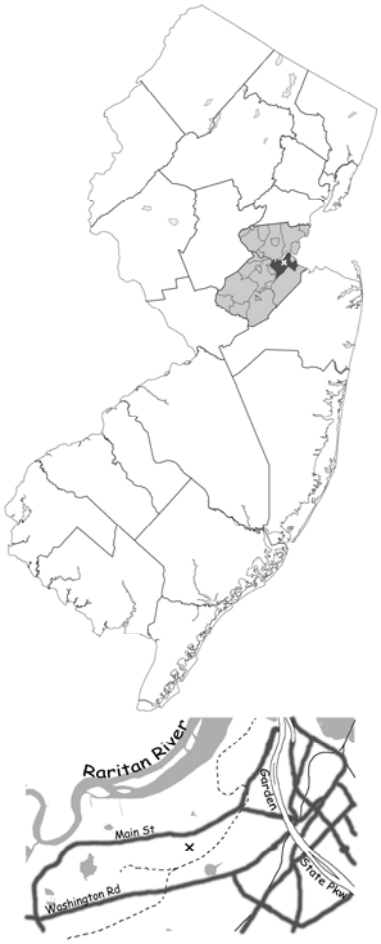


Figure 2.1. Location of the Old Crossman Clay Pit. White X marks the location within the State of New Jersey at the Sayreville Municipality (dark gray) in Middlesex County (light gray). Dark X marks the location within Sayreville, just south of the Raritan River.

The Atlantic Coastal Plain Geological Province consists of low-elevation sandy plains composed mostly of unconsolidated sands and clays without much structural deformation (Owens and Minard, 1960). The Raritan and Magothy formations probably represent fluvial/deltaic deposition environments (Christopher, 1979). The South Amboy Clay Member may represent the filling of old meanders that would correspond with a phase of marine regression (Christopher, 1979) or possibly a coastal lowland swamp (Sugarman et al., 2005). This member is characterized by white, red, and dark gray to black, irregularly interbedded, fine-grained, massive to laminated clays. Carbonized plant remains and wood are found in the dark beds (Owens et al., 1977), and small pieces of amber are also present (Sugarman et al., 2005). According to Christopher (1979), this member, along with most of the overlying Old Bridge Sand Member belong to the *Complexiopollenites exigua-Santalacites minor* Zone indicating a middle to late Turonian, possibly Coniacian age. A Turonian age estimate for the South Amboy Fire Clay had already been proposed by Groot et al. (1961), Doyle and Robbins (1977), and Christopher (1977) based on palynological evidence. However, stratigraphic correlation with other Atlantic and Gulf Coastal Plain sections, especially the Eagle Ford group of Texas has suggested a Coniacian-Santonian age (Christopher, 1982; Valentine, 1984). In this work, we will follow Christopher (1979) who defined the South Amboy Fire Clay as the stratotype for the *Complexiopollenites exigua-Santalacites minor* Zone with a Turonian age.

Fossil preparation— Bulk samples from the South Amboy Fire Clay were first dissolved in warm water. Once the clay lost its cohesiveness, the mixture was passed through a 0.500 mm aperture sieve (USA Standard Testing Sieve No. 35) stacked on top of a 0.212 mm aperture sieve (USA Standard Testing Sieve No. 70). This procedure eliminates most of the clay and the smaller sand from the matrix. To

remove the remaining clay, we soaked the concentrate for 2 h in detergent (Alconox) dissolved in warm water and then washed on the sieve stack several times. The concentrate was then left overnight soaking in warm water so the organic material (fossils) would float while the remaining sand would sink. These two components were separated by decanting. The organic component was immersed in 49% hydrofluoric acid (HF) and left for three nights to ensure the dissolution of the last adhering materials. The fossils were then rinsed in distilled water and air dried.

The fossils were observed and sorted under a Zeiss SV-11 stereomicroscope. The nine specimens that represent this taxon were mounted on SEM stubs and sputter-coated with gold/palladium to observe them in a field-emission Hitachi (Tokyo, Japan) S-4500 scanning electron microscope. All specimens are deposited in the L. H. Bailey Hortorium Paleobotany Collection, Department of Plant Biology, Cornell University with numbers CUPC-371, 579, 591 (counterpart of CUPC579), 642, 1171, 1467, 1565, 1650, 1663, and 1723. Two specimens (CUPC579 and CUPC1467) were dissected to study the internal structure of the flower, especially the ovules. Pollen was found within the anthers of only one specimen (CUPC642).

Fossil identification— To find possible familial affinities for the fossil taxon, three different taxonomic identification keys were applied: Hutchinson's (1973) *Families of Flowering Plants* (3rd ed.), Watson and Dallwitz' (1992 onward) *Families of Flowering Plants* and Kevin Nixon's *Families of Dicotyledons* (http://www.plantsystematics.org). Because the results from the keys suggested families that mostly fall within the order Theales of Cronquist (1981), each one of the 18 thealean families (sensu Cronquist) and each of the seven non-Thealean families also suggested by the keys (Aizoaceae, Dilleniaceae, Molluginaceae, Vivianaceae, Rutaceae,

Tamaricaceae, and Flacourtiaceae) were considered for comparison with the fossil. For this comparison, the family descriptions given by Cronquist (1981) and Takhtajan (1997) were used. Finally, the fossil was compared to dissected flowers (from Cornell Plantations) of the two families not discarded by the literature review, Theaceae s.l. and Clusiaceae s.l. (Hypericaceae).

Cladistic analysis— The fossil taxon was included in several phylogenetic analyses using different combinations of a slightly modified version of the Luna and Ochoterena (2004) morphological matrix, and the five molecular markers used by Prince and Parks (2001) and Yang et al. (2004): *rbcL*, *matK*, *trnL-trnF*, *matR*, and ITS. Details on each matrix are given later.

Each matrix analyzed was run 10 times in the program NONA version 2.0 (Goloboff, 1999) through the program Winclada version 1.00.08 (Nixon, 2002) and another 10 times in the program TNT (Goloboff et al., 2003, 2008). Each run consisted of 1000 replications of tree-bisection-reconnection (TBR) searches on randomly generated initial Wagner trees, holding up to 50 trees per replication with an additional TBR on the resulting trees (> h50000; rs0; h/50; mult*1000; max*). The trees obtained from the 10 different runs with a program were combined in Winclada, where suboptimal and duplicate trees were eliminated and a strict consensus tree was calculated from the resulting set of trees.

Standard bootstrap and jackknife values were calculated using TNT (Goloboff et al., 2003, 2008) on 1000 replications where each replication consisted of 10 TBR runs holding 10 trees and keeping only the strict consensus.

Morphology— The morphological matrix of Luna and Ochoterena (2004) includes 37 taxa and 60 characters. In their original analysis, Luna and Ochoterena treated characters 46 (number of ovules per locule) and 49 (number of styles) as additive; however, this information was accidentally omitted in the printed publication. In the current study, the two characters were changed back to additive giving a total of nine additive characters: vessel member length (character 9), indumentum (ch 13), petiole (ch 21), decurrent base of the leaf lamina (ch 22), corolla size (ch 26), stamen number (ch 33), extension of connective in the stamens (ch 38), ovules per locule (ch 46), and number of styles (ch 49). This matrix was reanalyzed to replicate and corroborate Luna and Ochoterena's results.

For the analysis with the fossil included, some changes were made to the morphological matrix (Table 2.1). The character state epitropous ovules of character 47 (ovule position) was deleted because it refers to a different attribute of the ovules than the remaining character states (orientation with respect to the ovary axis vs. curvature according to the relative positions of funiculus, micropyle, and chalaza) and is therefore not homologous to them.

In addition, a new morphological character, stamen height (ch 61), with four character states was defined. The state for each taxon was either observed (*Stewartia* and the fossil described here) or taken from the literature, primarily from Kobuski (1937, 1938, 1939, 1940, 1941a–c, 1942a, b, 1943, 1947, 1948, 1949, 1950a, b, 1951a–c, 1952a, b, 1956), Keng (1962, 1980, 1984, 1989), Weitzman (1987), Barker (1980), Morton et al. (1997) and Watson and Dallwitz (1992 onward). This character refers to the relative height of stamens in comparison with other stamens; the character states are (0) all equal, all stamens are the same height, all anthers are the

same level; (1) different heights laterally, in the same whorl, the heights of the stamens increase and decrease alternatively and gradually; (2) short and long, stamens in the same whorl are either short or long, no intermediates; (3) different heights in different whorls, stamens within the same whorl are the same height, but the heights change across whorls.

Molecular data— The molecular markers used here are the same ones (same accession numbers) used in the two analyses focused on the relationships within Theaceae s.l. Prince and Parks (2001) used the chloroplast *rbcL* and *matK*, while Yang et al. (2004) used the chloroplast *trnL-trnF*, the mitochondrial *matR*, and the nuclear region ITS (see Appendix). Because taxon sampling, especially in the outgroups, differs among studies, additional sequences were downloaded from Gen-Bank. Each gene was aligned in the program CLUSTAL_X (Thompson et al., 1997) using a gap-opening penalty of 20.00 and a gap-extension penalty of 5.00, then manually adjusted afterward.

Combined data— The five molecular data matrices were combined in Winclada and the taxa merged by genus following Luna and Ochoterena's (2004) circumscriptions (i.e., *Hartia* was included in *Stewartia*; *Laplacea*, *Franklinia*, and *Polyspora* were included in *Gordonia*). This made the molecular data set fully compatible and congruent in circumscription with the morphological one. Once morphological and molecular data sets were combined, the 10 outgroups represented in only one molecular data set were excluded from further analysis: *Anagallis*, *Diapensia*, *Diospyros*, *Elingamita*, *Impatiens*, *Lecythis*, *Manilkara*, *Polemonium*, *Styrax*, and *Theophrasta*. The resulting total evidence data matrix has 46 taxa (45 extant genera plus the fossil) and 8874 characters of which 1345 are informative.

Table 2.1. Matrix of morphological characters including the fossil taxon, *Pentapetalum*. Modified from Luna and Ochoterena (2004) , see text for details. Taxa names: TER-Ternstroemiaceae, THE-Theaceae s.s., TET-Tetrameristaceae, PEL-Pellicieraceae, KIE-Kielmeyeroideae (Clusiaceae), BON-Bonnetiaceae. Polymorphisms: A-[01], B-[02], C-[04], D-[12], E-[13], F-[23], G-[24], H-[012], I-[013], J-[023], K-[0123], L-[0234].

Character	1 5 10 15 20 25 30
Physena	1 0 0 0 0 1 0 0 ? 0 0 ? 0 ? 1 1 0 0 0 0 2 0 1 1 0 - 1 0 0 1 -
Actinidia	D 0 0 1 A A 2 1 1 1 0 0 B 0 1 1 0 A A 0 2 0 1 1 A 1 0 0 0 0 1
Adinandra-TER	1 0 0 0 1 1 B A 2 1 0 1 1 0 1 1 A A 0 A 1 1 0 1 1 D - 1 0 1 1
Anneslea-TER	1 0 0 0 1 1 B A 2 1 0 1 1 0 1 1 0 0 1 1 2 1 0 1 1 1 - 0 0 1 1
Apterosperma-THE	1 0 ? 0 1 1 B 1 2 1 0 ? 1 ? ? 1 0 0 1 0 2 ? 0 A 1 A - 0 0 1 1
Archboldiodendron-TER	1 0 0 0 1 1 B 0 2 1 0 1 1 0 1 1 A 0 1 0 1 1 0 1 1 1 - A 0 1 1
Archytaea-BON	A 1 A 0 0 0 B 0 0 1 0 1 0 1 0 1 0 0 1 0 A 1 0 1 AD 2 1 0 1 0
Asteropeia	1 0 ? 0 0 1 0 0 0 1 0 1 A ? ? 1 0 0 1 0 2 A 0 0 0 0 2 0 0 1 1
Balthasaria-TER	1 0 0 0 1 1 B 0 2 1 0 1 1 0 ? 1 A A 1 0 2 1 0 1 1 2 - 1 0 1 1
Bonnetia-BON	A 1 1 0 0 0 B 0 0 1 0 1 0 1 0 1 0 0 1 0 HA 0 1 ADD 1 0 1 0
Camellia-THE	1 0 0 0 1 1 J A 2 1 0 1 1 0 0 1 A A 1 0 HA 0 1 1 D - A 0 1 1
Caraipa-KIE	1 1 1 0 0 1 0 0 1 1 1 0 D 1 0 1 A 0 0 0 2 0 0 A 0 1 0 0 0 1 0
Cleyera-TER	1 0 0 0 1 1 B 1 2 1 0 1 1 0 1 1 1 A 1 0 2 1 0 1 1 A - 1 0 1 1
Cornus	E 0 ? 0 1 0 2 0 HA 0 0 1 0 1 AAAA 0 2 0 AA 0 BH 0 0 AH
Dankia-THE	1 0 ? 0 ? ? ? ? ? ? 0 ? 1 0 ? 1 0 0 1 0 2 0 0 1 1 1 - 0 0 1 1
Eurya-TER	1 0 0 0 1 1 J A 2 1 0 1 1 0 1 1 A A 1 0 D 1 1 1 1 0 - 1 0 1 1
Euryodendron-TER	1 0 ? 0 1 ? C 0 2 1 0 ? ? 0 ? 1 0 1 1 0 2 1 0 1 1 0 - 1 0 1 1
Ficalhoa-TER	1 0 0 0 1 ? L 0 2 1 1 1 A 0 ? 1 0 1 1 0 2 1 0 1 0 0 0 0 0 1 1
Freziera-TER	1 0 A 0 1 AB 0 2 1 0 1 1 A 1 1 1 A 1 0 H 2 1 1 1 A - 0 0 1 1
Gordonia-THE	1 0 0 0 1 1 BA 2 1 0 1 A 0 A 1 AA 1 0 D 1 A 1 1 D - 0 0 1 1
Haploclathra-KIE	1 1 0 0 0 1 0 0 1 0 1 0 D 1 0 0 0 0 0 0 2 0 0 0 0 D 0 0 0 1 0
Kielmeyera-KIE	1 1 0 0 0 1 1 0 0 0 1 0 A 1 0 1 0 0 0 0 D 0 1 0 0 2 0 0 0 1 0
Mahurea-KIE	1 1 1 0 A 1 0 0 2 0 1 0 1 0 0 1 0 0 0 0 2 0 0 0 0 1 0 0 0 1 0
Marcgravia	D 0 1 1 A 1 G 0 AA 0 1 A 0 3 1 AA 0 AH 0 0 0 0 1 A 0 0 1 1
Marila-KIE	1 1 1 0 A 1 2 0 2 A 1 0 H 0 0 0 0 0 0 A 2 0 0 A 0 H 0 0 0 1 A
Neotatea-KIE	0 1 ? 0 A 1 B 0 2 0 1 0 1 0 0 1 0 0 0 0 A 0 0 0 0 2 1 0 0 1 0
Pelliciera-PEL	0 0 ? 1 0 ? 2 0 ? 0 0 1 0 0 2 1 0 0 1 0 A 1 0 1 1 3 - 0 1 0 1
Pentamerista-TET	A 0 ? 1 0 0 F 0 1 ? 0 1 0 ? 1 1 0 A 1 0 A 1 0 1 0 0 1 0 1 0 1
Pentaphylax	1 0 0 0 1 ? 2 1 2 ? 0 0 0 ? 0 1 0 0 A 0 2 0 0 A 0 0 1 0 0 0 1
Pyrenaria-THE	1 0 0 0 1 1 J 0 2 1 0 1 1 0 A 1 0 A 1 0 2 1 0 1 1 1 - A 0 1 1
Schima-THE	1 0 0 0 1 1 J A 2 1 0 1 A 0 0 1 0 A 1 0 2 1 0 1 1 D - A 0 1 1
Sladenia	1 0 0 0 1 ? J 0 2 1 0 1 1 0 1 1 0 1 1 0 2 0 0 1 0 0 0 0 0 1 1
Stewartia-THE	1 0 0 0 1 1 J 1 2 1 0 1 1 0 0 1 0 A 1 0 2 2 0 1 1 2 - A 0 1 1
Symplococarpon-TER	1 0 0 0 1 1 ? ? ? ? 0 1 1 0 1 1 1 A 1 0 2 1 0 1 1 0 - 1 0 1 1
Ternstroemia-TER	1 0 0 0 1 1 BA 2 1 0 1 1 0 1 1 0 A 1 1 D 1 A 1 1 A - A 0 1 1
Tetramerista-TET	1 0 ? 1 0 0 F 0 1 ? 0 1 0 ? 1 1 0 A 1 0 A 1 0 1 0 0 1 0 1 0 1
Visnea-TER	1 0 0 0 1 1 B 1 2 1 0 1 1 0 1 1 A 0 1 0 2 0 0 1 1 0 - 1 0 1 1
Pentapetalum	? 0 ? ? ? ? 0 0 1 1

Table 2.1. (Continued)

Character	35	40	45	50	55	60
Physena	A 0 1 0 0 0 0 1 ? 2 0 ? 0 0 1 1 1 1 0 2 1 - - 0 0 ? 0 ? ? 0					
Actinidia	1 D 0 1 A A 0 1 ? 0 ? ? 0 A 2 0 0 1 0 1 0 - 1 0 1 1 A 1 0 0					
Adinandra-TER	1 A 1 0 A 0 1 1 0 0 1 0 0 A 2 D 0 A 0 1 1 - 0 0 1 0 0 A 1 3					
Anneslea-TER	1 1 1 0 0 0 1 1 0 0 1 ? 1 0 1 1 0 0 1 1 2 - - 0 1 0 1 0 1 0					
Apterosperma-THE	1 0 1 0 0 0 0 1 ? ? ? 1 0 1 1 ? ? 0 1 0 1 1 - 0 ? 0 0 1 0 3					
Archboldiodendron-TER	1 1 1 0 0 0 1 1 ? ? ? ? 0 1 2 ? ? 1 0 1 1 - 0 0 1 ? 0 1 1 ?					
Archytaea-BON	0 D 0 0 A 0 0 0 1 0 0 ? 0 0 2 0 0 A 0 0 0 0 - A A 0 0 1 0 0					
Asteropeia	0 0 1 0 0 0 0 1 1 2 0 ? 0 0 1 0 0 A 0 0 1 1 - 0 0 ? 0 1 ? 0					
Balthasaria-TER	1 A 1 0 0 0 1 1 0 0 1 ? 0 1 2 ? ? 0 0 A ? ? 0 0 0 ? 0 1 1 0					
Bonnetia-BON	0 D 0 A 0 0 0 1 1 0 0 ? 0 0 2 1 A A 0 0 A 0 - A 0 ? 0 1 0 3					
Camellia-THE	1 A 1 A 0 0 A 1 1 A 0 1 0 A 1 0 0 A 0 0 1 1 - 0 0 0 0 0 0 0					
Caraipa-KIE	0 2 0 1 0 0 2 0 A 0 0 ? 0 A 1 0 0 0 0 0 1 0 - 1 0 0 0 0 1 -					
Cleyera-TER	1 A 1 0 1 0 1 1 0 0 1 0 0 A 2 D 0 A 0 1 1 - A 0 0 0 0 1 1 1					
Cornus	0 0 1 1 1 0 0 1 1 0 1 ? 2 A 0 0 A A 0 3 1 - - 0 1 1 0 A ? -					
Dankia-THE	? D 1 0 0 0 0 1 ? ? ? ? 0 1 1 ? ? 1 0 0 1 1 - ? ? ? 0 ? ? -					
Eurya-TER	1 0 1 0 0 0 1 1 0 A 1 0 0 A 1 D 0 1 0 1 1 - 0 0 0 0 0 1 1 0					
Euryodendron-TER	1 0 1 0 1 0 1 1 ? ? ? ? 0 1 2 ? ? 0 0 1 1 - 0 0 ? ? 0 1 ? -					
Ficalhoa-TER	1 0 0 0 0 1 0 0 0 1 1 ? 0 1 2 ? ? 1 0 0 1 1 - 0 0 ? 0 1 0 -					
Freziera-TER	A A 1 0 0 0 1 1 0 0 1 ? 0 A 2 ? 0 0 1 1 1 - 0 0 0 0 0 1 1 2					
Gordonia-THE	A D A 1 0 0 A 1 1 0 0 1 0 A D 0 0 A A 0 A 1 - 1 0 0 0 0 0 I					
Haploclathra-KIE	0 1 0 0 0 0 0 0 A 0 0 ? 0 A 0 0 0 0 0 0 0 0 - 1 0 0 0 0 0 -					
Kielmeyera-KIE	0 D 0 1 0 0 B 0 1 0 A ? 0 0 2 0 0 0 0 0 0 0 - 1 1 0 0 0 0 -					
Mahurea-KIE	0 2 0 0 0 0 2 0 1 0 0 ? 0 0 2 0 0 0 0 0 0 0 - 0 1 0 0 1 0 -					
Marcgravia	2 A 1 A 1 0 0 1 0 A 1 ? 0 0 2 0 0 0 1 0 1 A - 0 0 1 A 1 ? -					
Marila-KIE	0 D 0 0 0 A 2 0 A 0 0 ? 0 A 2 0 0 0 0 0 0 0 - 0 1 0 0 1 0 -					
Neotatea-KIE	0 D 0 0 0 0 2 1 1 0 0 ? 0 0 2 0 0 0 0 0 0 0 - 1 0 0 0 1 0 -					
Pelliciera-PEL	0 0 1 0 0 0 1 1 1 0 1 ? 0 0 0 1 ? 0 0 2 3 - - 0 0 ? 1 0 ? 0					
Pentamerista-TET	0 0 1 0 0 0 0 1 0 0 0 ? 0 0 0 0 ? 0 0 1 0 - 0 0 1 ? 0 A 0 -					
Pentaphylax	0 0 1 0 ? 1 0 1 0 A 1 ? 0 0 1 A 1 0 A 0 1 1 - 1 0 ? 0 0 1 -					
Pyrenaria-THE	1 2 1 1 0 0 0 1 A 0 0 1 0 1 1 0 0 1 0 A A A 1 0 0 0 0 0 0 0					
Schima-THE	1 D 1 0 0 0 0 1 1 0 0 1 0 1 1 1 0 0 1 0 1 1 - 1 0 0 0 0 1 -					
Sladenia	1 0 1 0 1 1 0 1 0 0 1 ? 0 0 1 0 0 0 1 0 0 0 - 1 0 ? 0 1 0 0					
Stewartia-THE	1 D 0 1 0 0 0 1 1 0 0 1 0 1 1 ? 0 A 0 0 1 1 - A 1 0 0 0 0 1					
Symplococarpon-TER	1 A 1 0 0 0 1 1 0 0 1 ? 1 A 1 ? ? 1 0 1 2 - - 0 0 0 0 A 1 0					
Ternstroemia-TER	1 D 1 0 0 0 A 1 0 0 1 0 0 0 1 A 0 A 0 1 1 - A 0 1 0 1 A 1 K					
Tetramerista-TET	0 0 1 0 0 0 0 1 1 0 0 ? 0 0 0 0 ? 0 0 1 0 - 0 0 1 ? 0 0 0 -					
Visnea-TER	1 0 1 0 0 0 1 1 0 0 1 ? 1 1 D ? 0 1 0 1 2 - - 0 1 0 0 1 1 1					
Pentapetalum	0 1 1 0 0 0 0 ? 0 1 1 ? 0 0 1 0 ? 1 0 ? ? ? ? ? ? ? ? ? 1					

Four subset matrices were derived from this matrix, giving a total of five data sets to analyze: (1) total evidence (morphology + the five genetic regions), (2) total evidence with the six taxa belonging to the Kielmeyeroideae (Clusiaceae) excluded: 40 taxa, 1179 informative characters of 8874, (3) morphology + organelle genetic regions (*rbcL*, *matK*, *trnL-F*, *matR*): 46 taxa, 1042 informative characters of 7984, (4) morphology + chloroplast genetic regions (*rbcL*, *matK*, *trnL-F*): 46 taxa, 907 informative characters of 5310, and (5) morphology only: 38 taxa, 61 characters, all informative. A second version of each matrix, with the fossil excluded, was analyzed and compared to its counterpart to assess the effect of the fossil in the cladogram.

SYSTEMATICS

Order— Theales sensu Cronquist (1981) / Ericales sensu APG (2003)

Family— Theaceae sensu lato / insertae sedis

Genus— *Pentapetalum* Martínez-Millán, Crepet et Nixon, gen. nov.

Type species— *Pentapetalum trifasciculandricus* Martínez-Millán, Crepet et Nixon, sp. nov.

Etymology— The generic name refers to the presence of five petals that form the corolla.

Generic diagnosis— Flowers bisexual, pentamerous, actinomorphic, and with a flat, wide, somewhat triangular receptacle. Calyx and corolla well differentiated, sepals and petals free from one another. Androecium of numerous tetrasporangiate stamens grouped in three clusters that resemble fascicles. Filaments longest at the cluster's center and decrease in size laterally. Gynoecium tricarpellate with three distinct styles. Ovary trilocular with axile placentation. This genus can be easily distinguished among the fossil flowers of the Raritan Formation primarily by its

numerous nonlaminar stamens of unequal sizes. Although very similar to extant *Stewartia* and *Gordonia*, it differs in having a tricarpellate gynoecium.

Generic description— Flowers bisexual, actinomorphic, hypogynous, somewhat triangular in shape (top view) with a more or less flat wide receptacle. Calyx of five quincuncially arranged sepals. Corolla of five petals with imbricate arrangement. Androecium of numerous stamens borne in one cycle but grouped in three clusters that resemble fascicles. In each cluster, the filaments are longest at the center and decrease in size laterally on each side. The anthers are tetrasporangiate and basifixed. Pollen grains triaperturate, apparently tricolporoidate. Gynoecium of three fused carpels with three distinct styles. Ovules anatropous, arranged in two rows along the axile placentae.

Pentapetalum trifasciculandricus Martínez-Millán, Crepet et Nixon, sp. nov.

—*Holotype*— part CUPC579 (Figs. 2.2, 2.3, 2.8, 2.13, 2.14, 2.17) and counterpart CUPC591 (Fig. 2.4)

Paratypes— CUPC371, CUPC642 (Figs. 2.5, 2.6, 2.12, 2.18, 2.19, 2.20), CUPC1171 (Fig. 2.7), CUPC1467 (Fig. 2.16), CUPC1565 (Fig. 2.10), CUPC1650 (Figs. 2.11, 2.15), CUPC1663, CUPC1723 (Fig. 2.9)

Locality— Old Crossman Clay Pit, Sayreville, New Jersey, USA (Fig. 2.1).

Stratigraphy— South Amboy Fire Clay, Raritan Formation

Age— Turonian, Late Cretaceous

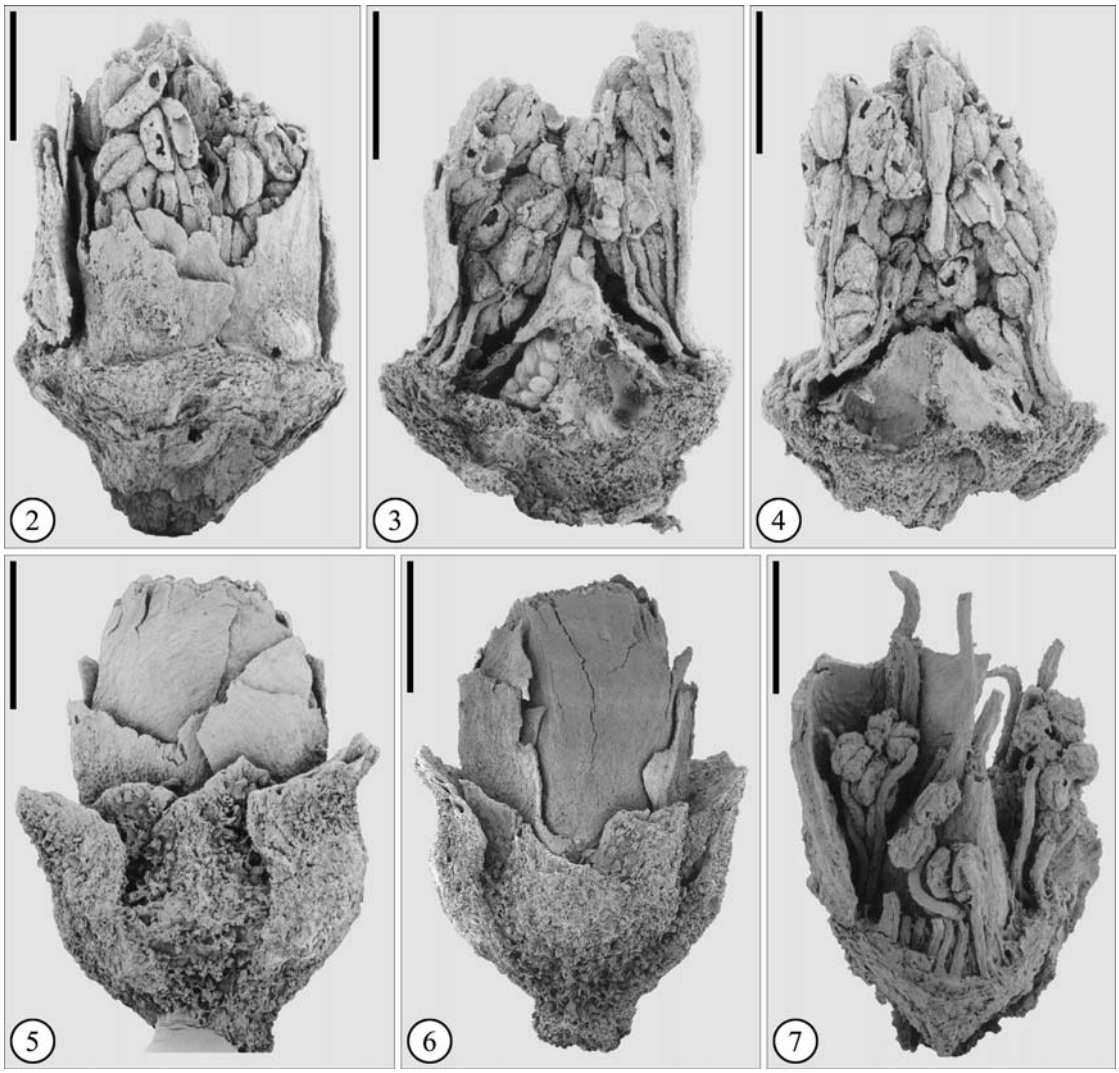
Etymology— The specific epithet refers to the arrangement of the androecium, in three groups that resemble fascicles or bundles

Specific diagnosis— As for the genus.

Specific description— *Pentapetalum trifasciculandricus* is known from nine specimens. The flowers are between 1.36 and 1.95 mm long (mean 1.63 mm) and

between 0.82 and 1.38 mm wide (mean 1.06 mm). The perianth is well differentiated into calyx and corolla (Figs. 2.5, 2.6). The calyx is formed of five quincuncially arranged distinct sepals (Figs. 2.8–2.10). From the base of the flower to the tip of the sepals, the calyx measures between 1.10 and 1.18 mm (mean 1.14 mm). The corolla of five distinct imbricate petals (Figs. 2.2, 2.5, 2.6) measures around 1.34 mm long and between 0.96 and 1.69 mm wide. Each petal wraps around covering between 187.6° and 335° of the bud's circumference at its widest (Figs. 2.8–2.10, 2.12). The stamens are numerous and clustered in three groups (Figs. 2.7–2.9), with filaments free except basally where adnate to the petals (Figs. 2.13–2.15). Each group is formed by at least 10 stamens of markedly different heights with their filament lengths decreasing outward from the center (Fig. 2.13). Filaments and anthers well differentiated. The longest filament is 0.73 mm long, while the shortest is 0.18 mm. Anthers tetrasporangiate and basifixed (Figs. 2.2–2.4, 2.13), between 0.14 and 0.25 mm long (mean 0.19 mm). One specimen, CUPC-642, bears in situ pollen grains that appear to be tricolporoidate (Figs. 2.18–2.20). Pollen grains are around 13.35 μm long and 12 μm at the equator with little ornamentation (Fig. 2.20). Gynoecium superior, syncarpous with free styles ("synovarious" of Watson and Dallwitz [1992]) formed by three carpels (Figs. 2.3, 2.4, 2.7, 2.11). Styles three, apically inserted on the ovary, free for their entire length (at least 0.75 mm long) and with presumably one stigma per style (Fig. 2.7). Ovary trilocular with complete septa (Figs. 2.11, 2.16), between 0.32 and 0.39 mm tall (mean 0.35 mm) and 0.58 and 0.86 mm wide at the base (mean 0.70 mm). Ovules several per locule (about eight) organized in two rows on the axile placenta (Fig. 2.17). Ovules are globose in shape, between 61.8–62.5 μm long and 42.1–45.8 μm wide. Fruits unknown. No vegetative parts or inflorescences are known.

Figures 2.2-2.7. *Pentapetalum trifasciculandricus*. **2.2**. Lateral view of holotype (CUPC579) showing five imbricate petals (sepals removed) and multiple stamens (bar = 400 μm, 70X). **2.3**. Longitudinal section of holotype (CUPC579) showing superior ovary and ovules in two rows (bar = 400 μm, 70X). **2.4**. Longitudinal section of holotype counterpart (CUPC591) showing ovary with two locules and one septum and multiple stamens. (bar = 400 μm, 70X). **2.5**. Lateral view of CUPC642 ("front") showing five imbricate petals and three of the five quincuncial sepals (bar = 600 μm, 50X). **2.6**. Lateral view of CUPC642 ("back") showing the five petals and the other two sepals (bar = 600 μm, 50X). **2.7**. Lateral view of CUPC1171 showing the three styles departing from the syncarpous ovary and stamens in three groups (bar = 300 μm, 100X).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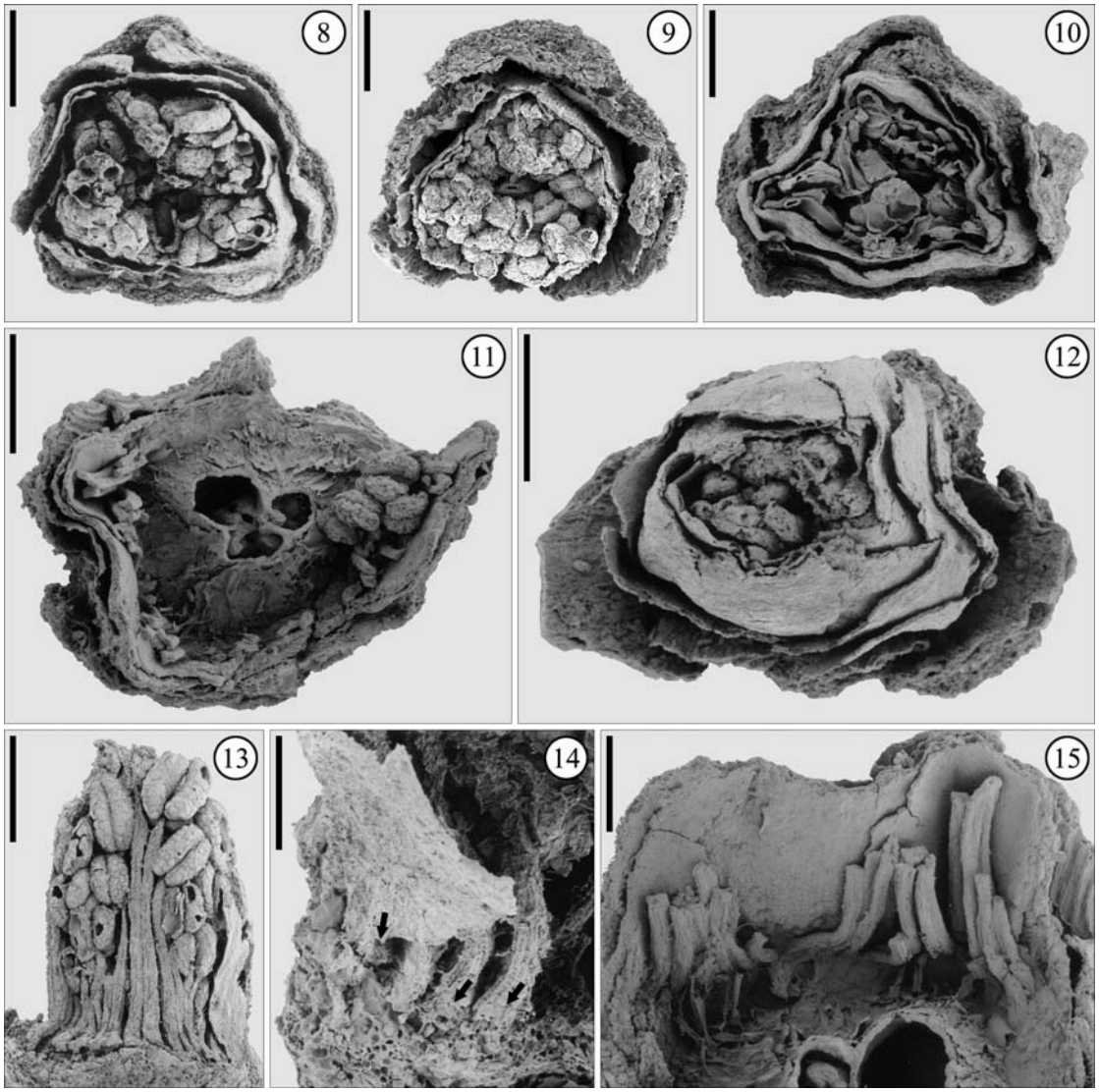
Figures 2.8-2.15. *Pentapetalum trifasciculandricus*. **2.8**. Top view of holotype (CUPC579) showing the three groups of stamens and imbricate perianth (bar = 300 μm, 80X). **2.9**. Top view of CUPC1723 showing quincuncial aestivation of sepals (bar = 300 μm, 70X). **2.10**. Top view of CUPC1565 showing the triangular shape of the receptacle (bar = 300 μm, 70X). **2.11**. Top view of CUPC1650 showing the trilocular ovary with axial placentation (bar = 400 μm, 60X). **2.12**. Top view of CUPC642 showing two prominent sepals (outermost sepals) and large imbricate petals (bar = 400 μm, 70X). **2.13**. Holotype (CUPC579, "back" of Fig. 2.3) with petals removed to show one of the three groups of stamens; filaments become shorter as they depart from the "center" of the group (bar = 300 μm, 110X). **2.14**. Close up of longitudinal section of holotype (CUPC579, Fig. 2.3) showing attachment of stamens; the scars (arrows) indicate the place where the petal was attached to the filament (bar = 100 μm, 250X). **2.15**. Close up of CUPC1650 (Fig. 2.11) showing attachment of stamens to the petals at the base (bar = 200 μm, 110X).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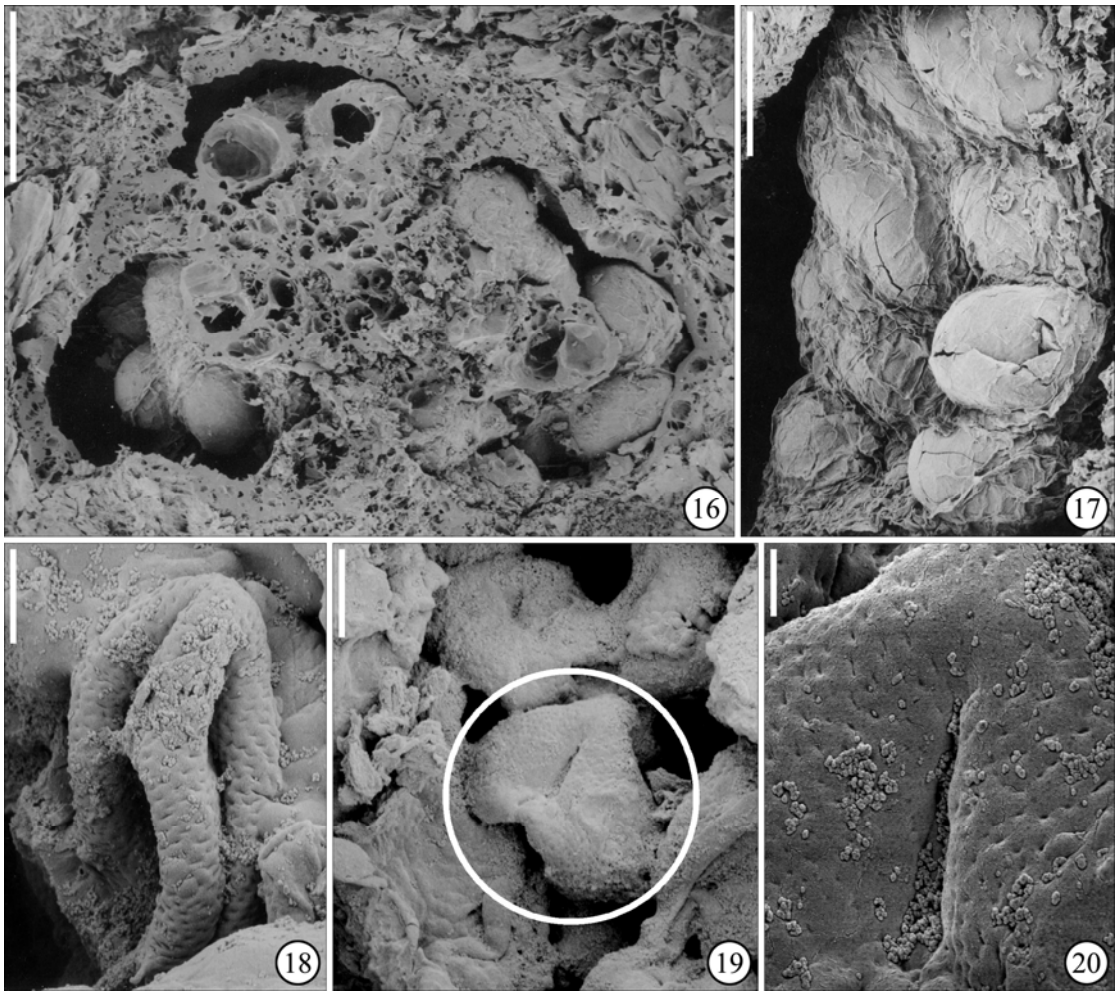
Figures 2.16-2.20. *Pentapetalum trifasciculandricus*. **2.16**. Cross section of the ovary of CUPC1467 showing three locules with axile placentation and ovules in two rows (bar = 100 μm, 250X). **2.17**. Close up of longitudinal section of holotype (CUPC579, Fig. 2.3) showing ovules in two rows inside a locule (bar = 50 μm, 600X). **2.18**. Close up a pollen grain from CUPC642 (bar = 3 μm, 7000X). **2.19**. Pollen grains in situ, inside an anther of CUPC642, circle surrounds one pollen grain (bar = 5 μm, 2500X). **2.20**. Close up of circled pollen grain of Fig. 2.19 (CUPC642) showing aperture and wall ornamentation (bar = 1 μm, 18000X).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RESULTS

Fossil identification— The three identification keys yielded similar results; all of them suggested a set of families as possible matches for the fossil rather than a single family. Hutchinson's (1973) *Families of Flowering Plants* (3rd ed.) resulted in Theaceae, Dilleniaceae, Rutaceae, Tamaricaceae, Flacourtiaceae (*Prockia*), Aizoaceae, Hypericaceae, and Clusiaceae. Watson and Dallwitz' (1992 onward) *Families of Flowering Plants* suggested Aizoaceae, Dilleniaceae, Molluginaceae, Quiinaceae, Theaceae, and Vivianaceae. Nixon's *Families of Dicotyledons* (available at http://www.plantsystematics.org) resulted in Clusiaceae, Fouqueriaceae, Olacaceae, Rosaceae, Saxifragaceae, and Aizoaceae. Because many of the families suggested by the keys fall into the order Theales sensu Cronquist (1981), all the families in that order were added to the list giving a total of 25 families to review: Ochnaceae, Sphaerosepalaceae, Sarcolaenaceae, Dipterocarpaceae, Caryocaraceae, Theaceae, Actinidiaceae, Scytopetalaceae, Pentaphylaceae, Tetrameristaceae, Pelliceriaceae, Oncothecaceae, Marcgraviaceae, Quiinaceae, Elatinaceae, Paracryphiaceae, Medusagynaceae, Clusiaceae, Aizoaceae, Dilleniaceae, Molluginaceae, Vivianaceae, Rutaceae, Tamaricaceae, and Flacourtiaceae.

The literature review excluded most of the families except for the Theaceae s.l. and the Clusiaceae s.l. (Hypericaceae). However, comparison of the fossil flowers to the flowers and flower buds of *Stewartia pseudocamellia* (Theaceae s.l.) and *Hypericum* sp. (Hypericaceae) showed that the fossils shared more characters with the Theaceae s.l. than with the Hypericaceae (Table 2.2).

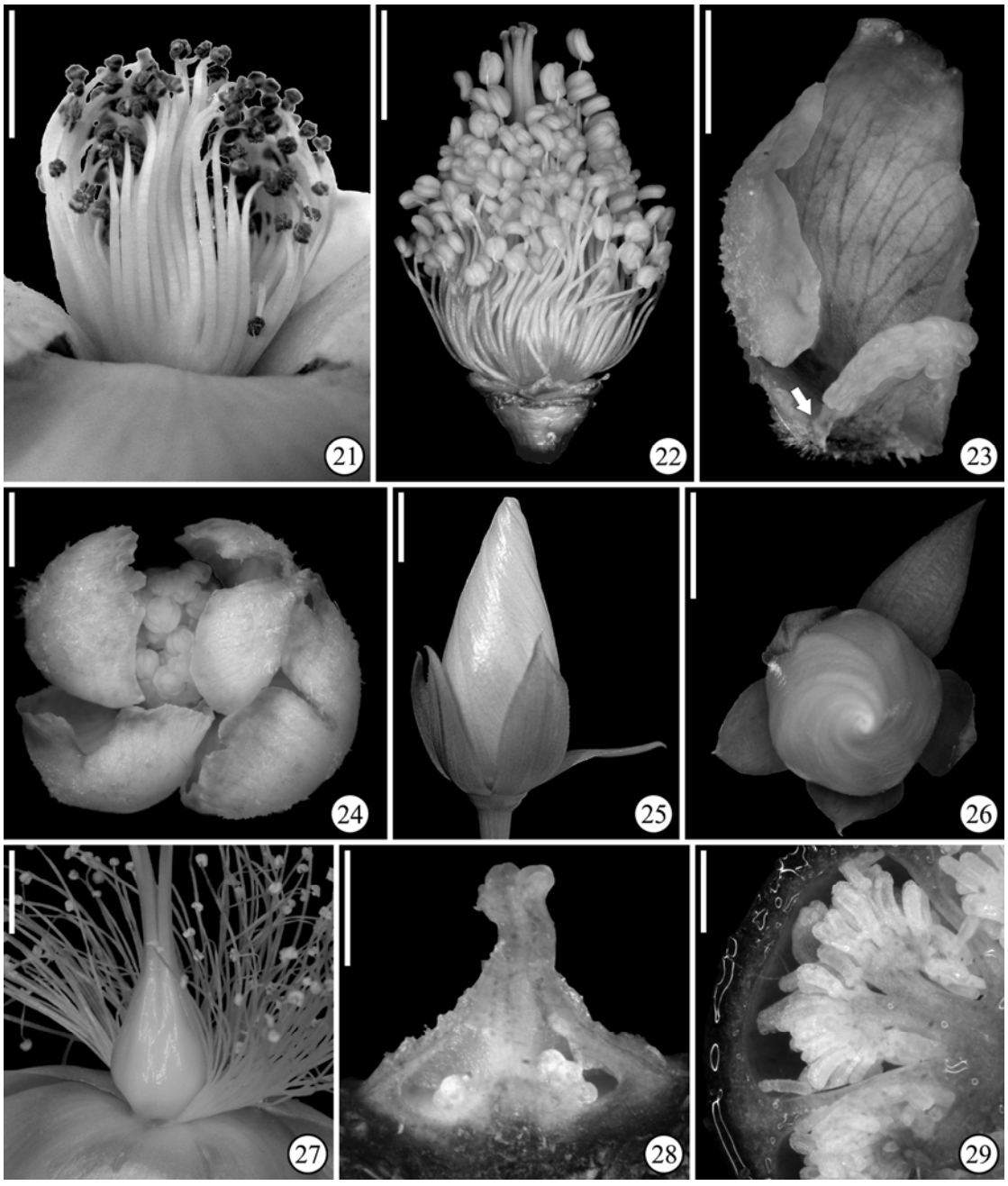
Table 2.2. Comparison of morphological characters observed in the fossil taxon (*Pentapetalum*) and two extant members of Theaceae (*Stewartia*) and Hypericaceae (*Hypericum*).

Character	*Stewartia*	*Pentapetalum*	*Hypericum*
Calyx aestivation	quincuncial	quincuncial	valvate
Attachment of sepal to receptacle	not jointed	not jointed	jointed
Sepal midvein	absent	absent	present
Corolla aestivation	imbricate	imbricate	contorted
Stamen-petal adnation	basally	basally	absent
Stamens (true fascicles)	fascicled	not fascicled	fascicled
Stamen height	unequal	unequal	equal
Gland terminating the connective	absent	absent	present
Attachment of floral parts with respect to ovary	same level	same level	below
Ovary shape	teardrop	teardrop	flask
Styles	1	3	1/3/5
Carpels	5	3	3/5
Ovules per locule	several	several	many
Ovule shape	globose	globose	elongated

Some of the most distinctive characters found in *Pentapetalum* and *Stewartia* are the stamen height that varies laterally (Figs. 2.13, 2.21), the slight adnation of stamen bases to petals (Figs. 2.14, 2.15, 2.23), the quincuncial aestivation of the calyx (Figs. 2.5, 2.6, 2.8, 2.9, 2.12), and the imbricate aestivation of the corolla (Figs. 2.2, 2.5, 2.6, 2.8, 2.12, 2.24). In contrast, in *Hypericum* the stamens are of the same height (Fig. 2.22), the bases of the stamens are free of the petals (Fig. 2.22; removal of petals

did not disturb stamens), the calyx aestivation is valvate (Figs. 2.25, 2.26) and the corolla aestivation is contorted (Figs. 2.25, 2.26). Moreover, closer examination of the floral architecture of these three taxa reveals even more characters found in the fossil and in the Theaceae but not in the Hypericaceae: (1) The sepals of *Hypericum* show a midvein and a jointed attachment to the receptacle (Fig. 2.25) that neither *Pentapetalum* nor *Stewartia* possess (Figs. 2.5, 2.6). (2) A gland terminating the connective is found in the anthers of *Hypericum* (not shown) but not in those of *Pentapetalum* or of *Stewartia*. (3) The ovaries of *Stewartia* and *Pentapetalum* have a broad base and taper toward the styles in a teardrop shape, with the rest of the floral parts attached to the receptacle at the same level of the gynoecium (Figs. 2.7, 2.11, 2.15, 2.28); in contrast, the gynoecium of *Hypericum* has a narrow base, it broadens toward the middle of the ovary and then it tapers toward the style in the shape of a flask, with the rest of the floral parts attaching underneath it (Fig. 2.27). (4) Inside the ovary, the ovules of *Pentapetalum* and *Stewartia* are globose in shape and several per locule (Figs. 2.3, 2.16, 2.17, 2.28), while those of *Hypericum* are elongated and very numerous (Fig. 2.29). There are however, a couple of characters found in *Pentapetalum* and in some species of *Hypericum* but not in *Stewartia*: free styles (Figs. 2.7, 2.27; Coulter, 1886; Robson, 1978) and a tricarpellar gynoecium (Fig. 2.7, 2.11, 2.16, 2.27; Coulter, 1886; Robson, 1978); in *Stewartia* the single stylar column branches (Fig. 2.28) and the gynoecium is pentacarpellate (Fig. 2.22). On the other hand, both *Stewartia* and *Hypericum* have fascicled stamens (Fig. 2.21; Robson, 1978) while *Pentapetalum* has one cycle (Figs. 2.11, 2.15) with the stamens gathered in three groups (Fig. 2.8). Despite the few characters differing between *Stewartia* and *Pentapetalum*, the floral structure of the fossil taxon shows significantly more affinities with members of the Theaceae than with members of the Hypericaceae (Table 2.2).

Figures 2.21-2.29. Extant Theaceae and Hypericaceae. **2.21**. Lateral view of a flower of *Stewartia pseudocamellia* (Theaceae) showing lateral distribution of filament lengths (bar = 1 cm). **2.22**. Lateral view of a bud of *Hypericum sp* (Hypericaceae) with perianth removed showing laterally uniform filament lengths (bar = 5 mm). **2.23**. Lateral view of a young petal of *S. pseudocamellia* showing attachment of stamen bundle to petal at arrow (bar = 2 mm). **2.24**. Top view of a bud of *S. pseudocamellia* showing imbricate corolla aestivation, outermost petal removed (bar = 2mm). **2.25**. Lateral view of a bud of *Hypericum sp* showing contorted corolla aestivation and a valvate calyx with jointed attachment of the sepals and a distinctive midvein on them (bar = 5 mm). **2.26**. Top view of a bud of *Hypericum sp* showing contorted corolla aestivation and valvate calyx aestivation (bar = 5 mm). **2.27**. Lateral view of a flower of *Hypericum sp* with one stamen group removed showing flask-shaped ovary with a narrow base and floral parts attaching beneath it (bar = 5 mm). **2.28**. Longitudinal section of the young pistil of *S. pseudocamellia* showing superior teardrop-shaped ovary with broad base and few ovules per locule (bar = 1 mm). **2.29**. Cross section of a young ovary of *Hypericum sp* showing numerous elongated ovules per locule in numerous rows (bar = 1 mm).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Cladistic analysis— Our analysis of the morphological matrix of Luna and Ochoterena (2004) resulted in 94 cladograms in contrast to the 45 they reported. However, the strict consensus is identical to the one they obtained (not shown), suggesting that the additional trees we found represent alternative arrangements to unsupported branches. Once this analysis was corroborated, the morphological matrix was modified and combined with the molecular markers. Alignment of these molecular markers was straightforward except for ITS where, despite being easily alignable among closely related taxa (members of Ericales, Cornales, and Kielmeyeroideae), large gaps had to be added to align the Ericales with the Cornales and with the Kielmeyeroideae.

The analysis of the total evidence matrix as well as of some of its subsets resulted in arrangements consistent with previous molecular analyses of larger taxonomic scope (i.e., Soltis et al., 2000; Bremer et al., 2002); the caryophyllid taxa *Physena* (functional outgroup) and *Asteropeia* are outgroups to a clade formed by the rest of the taxa included in the analysis (Figs. 2.30–2.32). Within the latter, there is a rosid (malpighioid) clade represented by the eight taxa in the Clusiaceae subfamily Kielmeyeroideae (KIE) and the two taxa of the Bonnetiaceae (BON), and an asterid clade represented by members of the Cornales (*Cornus* and *Hydrangea*) and Ericales (everything else) sensu APG (1998, 2003) (Figs. 2.30–2.32). Within the Ericales, the different clades found are consistent with the results of the more inclusive molecular analysis of Schönenberger et al. (2005). The morphological matrix, however, differs significantly from this arrangement because *Asteropeia* and the rosid clade are intermixed with the asterid taxa (Fig. 2.33).

Figures 2.30-2.33. Strict consensus of the most parsimonious trees obtained after collapsing unsupported branches. Numbers in branches based on 1000 replications, values <50% not shown, value 100% represented by 00: above branch = bootstrap, below branch = jackknife, black = with fossil included in the matrix, gray = with fossil excluded. **2.30**. Strict consensus of 32 trees (L = 4552, CI = 72, RI = 72 each), morphology + five genetic regions (*rbcL*, *matK*, *trnL-F*, *matR*, ITS). Arrows indicate the three nodes that collapse when the analysis is repeated without the six members of the Kielmeyeroideae (bootstrap and jackknife values not shown but very similar to the ones obtained when these taxa are included). **2.31**. Strict consensus of 1616 trees (L = 3633, CI = 72, RI = 71 each), morphology + organelle genetic regions (*rbcL*, *matK*, *trnL-F*, *matR*). **2.32**. Strict consensus of 16 trees (L = 3262, CI = 70, RI = 71 each), morphology + chloroplast genetic regions (*rbcL*, *matK*, *trnL-F*). **2.33**. Strict consensus of 27 trees (L = 230, CI = 35, RI = 65 each), only morphology.


Physena
Asteropeia
Archytaea-BON
Bonnetia-BON
Neotatea-KIE
Mahurea-KIE
Marila-KIE
Kielmeyera-KIE
Caraipa-KIE
Haploclathra-KIE
Cornus
Hydrangea
Ficalhoa-TER
Fouquieria
Marcgravia
---> Pentapetalum
Pentaphylax
Sladenia-TER
Symplocos
Pelliciera-PEL
Pentamerista-TET
Tetramerista-TET
Anneslea-TER
Ternstroemia-TER
Freziera-TER
Balthasaria-TER
Cleyera-TER
Adinandra-TER
Archboldiodendron-TER
Euryodendron-TER
Eurya-TER
Symplococarpon-TER
Visnea-TER
Actinidia
Cliftonia-CYR
Cyrilla-CYR
Dankia-THE
Rhododendron
Sarracenia
Clethra
Stewartia-THE
Schima-THE
Apterosperma-THE
Pyrenaria-THE
Camellia-THE
Gordonia-THE
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31
32
33

Only eight clades are constant across analyses because they are found in all of the consensuses (Figs. 2.30–2.33): Tetrameristaceae (TET), Pellicieraceae-Tetrameristaceae (PEL-TET), *Anneslea-Ternstroemia* (TER), *Adinandra-Archboldiodendon* (TER), Bonnetiaceae (BON), *Mahurea-Marila* (KIE), Kielmeyeroideae (KIE), and Bonnetiaceae-Kielmeyeroideae (BON-KIE) with the last three present in all analyses that include those taxa (Figs. 2.30–2.33). When only the analyses with molecular characters are considered (Figs. 2.30–2.32), eight additional clades are constant: rosids-asterids, a clade including *Actinidia*, *Cliftonia*, *Cyrilla*, *Dankia*, *Rhododendron*, and *Sarracenia*; a clade including all sampled Ternstroemiaceae excluding *Ficalhoa* (TER) and *Sladenia* (TER); a clade nested within it that excludes *Anneslea* and *Ternstroemia* (TER); and the Theaceae s.s. excluding *Dankia* (THE) with the structure: (*Stewartia* (*Schima* (*Apterosperma* (*Gordonia-Camellia-Pyrenaria*)))). The Cornales clade and the asterid clade collapse in the total evidence analysis when the Kielmeyeroideae is excluded (Fig. 2.30) but are otherwise present in all combined molecular + morphological analyses (Figs. 2.30–2.32). The Ericales are monophyletic only on the total evidence analysis with all taxa (Fig. 2.30) and in the morphology + organelle regions analysis (Fig. 2.31).

The most inclusive analysis, total evidence with all taxa (Fig.2.30), shows the fossil taxon as a member of the Ericales clade sensu APG (1998, 2003), but its position within this clade is unresolved because it is found in a polytomy with six other genera and three clades. A closer look at the resulting 32 most parsimonious trees (MPTs) (Fig. 2.30) shows that there were two preferred positions for the fossil: as sister to *Marcgravia*, supported by small pollen grains (ch 40 state 0: polar axis < 30 μm) or around the basal part of an extended Ternstroemiaceae clade that includes *Ficalhoa*, *Sladenia*, and *Pentaphylax* and corresponds to Schönenberger et al's (2005)

Pentaphylacaceae (alternative placements within this clade are as sister to *Pentaphylax* supported by free petals [ch 32 state 0], as sister to *Ficalhoa* supported by tricolporoidate aperture [ch 41 state 1] and more than one style [ch 49 state 1], or as sister to the *Anneslea*-to-*Visnea* clade supported by 30–70 stamens [ch 33 state 1]). The exclusion of the fossil from the analysis results in higher bootstrap and jackknife values for some clades (Fig. 2.30) and resolution of the basal ericalean polytomy, but the rest of the relationships remain unchanged.

The strict consensus of the morphology + organelle regions analysis (Fig. 2.31) shows the same structure as the total evidence analysis except that the Kielmeyeroideae and the Ternstroemiaceae clades lose almost all internal resolution. The different resolutions to these polytomies account for the high number of MPTs (Fig. 2.31). Close examination of these 1616 MPTs shows that *Pentapetalum* is placed in the same positions as in the total evidence analysis, as sister to *Marcgravia* or in the basal part of the extended Ternstroemiaceae clade, supported by the same characters already discussed. Removal of the fossil from the matrix results, as in the total evidence analysis, in higher bootstrap and jackknife scores for some clades (Fig. 2.31) and resolution of the basal ericalean polytomy.

In contrast, the morphology + chloroplast regions analysis (Fig. 2.32) shows more resolution when the fossil is included in the analysis than when it is excluded. In this analysis, the preferred position for the fossil is as sister to *Pentaphylax* (Fig. 2.32) with free petals (ch 31 state 0) as the synapomorphy that supports the relationship. When the fossil is excluded, some bootstrap and jackknife values increase while others decrease (Fig. 2.32) and some resolution is lost at the base of the Cornales' sister group, a clade that includes all ericalean taxa except the Marcgraviaceae-

Pellicieraceae-Tetrameristaceae branch and that is equivalent to Schönenberger et al.'s (2005) group I.

The morphological analysis, on the other hand (Fig. 2.33) shows relationships that conflict with all the analyses that include molecular data. However, this strict consensus conforms with older ideas of phylogenetic relationships, common in classification schemes based on morphology alone. For example, the Theaceae s.l. (Theaceae s.s. + Ternstroemiaceae excluding *Pentaphylax* and *Sladenia*) is monophyletic in this analysis (Fig. 2.33), and the Bonnetiaceae-Kielmeyeroideae clade is nested within a clade composed of many taxa that Cronquist (1981) and Takhtajan (1997) would place in their respective order Theales and superorder Theanae. A closer look at the 27 cladograms obtained from this analysis finds three preferred places for *Pentapetalum*: as sister to a clade composed by *Actinidia*, *Cornus*, *Marcgravia*, *Pentaphylax*, and *Sladenia* by means of sharing a smooth supratectal ornamentation (ch 42 state 1), as sister to only *Marcgravia-Pentaphylax-Sladenia* supported by pollen grains with polar axis smaller than 30 μm (ch 40 state 0), or as sister to a clade composed by the Theaceae s.l. and the rosid groups (KIE-BON-THE-TER) supported by 30–70 stamens (ch 33 state 1). Removal of the fossil from the analysis results in improved bootstrap and jackknife scores but not of resolution. This analysis (morphology without fossil) is largely similar to Luna and Ochoterena's (2004) analysis, but due to the added character (ch 61: stamen height) and the eliminated character state (ch 47: ovule position), it is not identical to theirs. However, the consensus trees are very similar, with the only difference that the *Stewartia-Gordonia* clade collapsed in our analysis.

In general, our different cladistic analyses placed the fossil close to *Marcgravia* or around the Ternstroemiaceae and *Pentaphylax*, which is sometimes itself placed with Ternstroemiaceae. These results contrast with those from direct observations, which suggested a closer affinity with the Theaceae s.s. (*Stewartia*).

DISCUSSION

Pentapetalum has a generalized morphology reminiscent of the families that Cronquist (1981) placed in his order Theales. The flower is actinomorphic with presumably showy petals and numerous stamens that, at least in gross appearance, are clustered in groups. This general plan is found in several of those Thealean families of Cronquist (1981) , for example, Actinidiaceae, Clusiaceae (including Hypericaceae), Theaceae s.l. (incl. Ternstroemiaceae), Medusagynaceae, and Quiinaceae among others. However, recent molecular analyses (i.e., Soltis et al., 2000; Bremer et al., 2002) have proven that many of these families are distantly related and that this floral plan is not homologous. These observations were corroborated when the fossil was subjected to three different identification keys, all of which independently suggested families belonging to Cronquist's order Theales, families now placed in APG's order Ericales (Theaceae [+ Ternstroemiaceae]) or Malpighiales (Clusiaceae [+Hypericaceae]).

Direct observations of members of the families suggested by the keys and the literature review showed that the floral architecture of *Pentapetalum*, whorl by whorl, is more congruent with that of the Theaceae (*Stewartia pseudocamellia*) than that of the Hypericaceae (*Hypericum* spp.). The number of characters that *Pentapetalum* shares with *Stewartia* is significantly larger than the number it shares with *Hypericum* (Table 2.2), supporting the notion that *Pentapetalum* has thealean affinities. However,

despite the remarkable similarity between the fossil flowers and *Stewartia*, it would be premature to assign the fossil to this genus or even to this family without the critical and rigorous test of phylogenetics (Crepet, 2008)—not only because the only diagnostic character for the Theaceae s.s. (presence of pseudopollen in the connective [ch 43; Tsou 1997, 1998]) could not be verified in the fossil, but also because the monophyly and the synapomorphies for the Theaceae have not been confidently established (compare Prince and Parks [2001] with Luna and Ochoterena [2004]).

The phylogenetic analyses performed did not completely agree with the direct observations because *Pentapetalum* was not placed close to *Stewartia* in any of the cladograms (Figs. 2.30–2.33). However, the analyses did suggest relationships between *Pentapetalum* and former members of the Theaceae s.l.: the Ternstroemioidae (Keng, 1962)/Ternstroemiaceae (Weitzman et al., 2004)/Pentaphylacaceae (APG, 2003; Schönenberger et al., 2005). In some of the cladograms resulting from analyses that included molecular and morphological characters (Figs. 2.30–2.32), *Pentapetalum* was sister to *Pentaphylax*, but in others it was sister to *Ficalhoa*, and in others it was sister to a clade of all Ternstroemiaceae except *Ficalhoa* and *Sladenia*. All these groupings are consistent with a generalized thealean floral structure. In contrast, the analysis with only morphological characters places *Pentapetalum* as sister to a clade including *Cornus*, *Actinidia*, *Pentaphylax*, *Sladenia*, and *Marcgravia*, a clade of the latter three, or a clade including all Theaceae s.l. + Bonnetiaceae-Clusiaceae. Although the phylogenetic relationships suggested by the morphology-only tree (Fig. 2.33) conflict with those suggested by the combined morphology + molecular trees (Figs. 2.30–2.32), *Pentapetalum* is still preferably placed close to members of the Ternstroemioideae/Ternstroemiaceae/ Pentaphylacaceae.

The alternative placement of *Pentapetalum* in the total evidence (Fig. 2.30; morphology, *rbcL*, *matK*, *trnL-F*, *matR*, and ITS) and in the morphology + organelle regions (Fig. 2.31; morphology, *rbcL*, *matK*, *trnL-F*, and *matR*) analyses as sister to *Marcgravia* is supported by small pollen grains (polar axis < 30 μm), a character state that also supports the Ternstroemiaceae clade (Fig. 2.30) in these trees. The character state for most of the Theaceae s.s. is large pollen grains (polar axis > 30 μm). However, for the rest of the taxa between these two clades, this character was coded as unknown, raising the possibility that small pollen grains could be a symplesiomophy instead of a synapomorphy of two clades. To test this, it would be necessary to collect data from those taxa for which this character is unknown.

The combined analysis of morphology and chloroplast regions (*rbcL*, *matK*, and *trnL-F*), on the other hand, always placed *Pentapetalum* as sister to *Pentaphylax*, and these as sister to the Ternstroemiaceae excluding *Ficalhoa* and *Sladenia*, which are placed in a very distant position (Fig. 2.32), reinforcing the idea of thealean affinities for the fossil.

One of the problems in assessing with confidence the phylogenetic relationships of this fossil is the lack of support for many of the branches of the trees (Figs. 2.30–2.33), not only in branches that lead directly to the fossil but in others as well, for example, all internal branches within Theaceae s.s. and many basal branches within the Ericales (Fig. 2.32). However, contrary to popular belief, this lack of support is not due to the presence of the fossil in the matrix, but to conflicting signals among the different partitions involved. Repetition of each analysis with the fossil removed from the matrix resulted in little or no increase of support for clades that

already had support, but clades without support, remained unsupported (Figs. 2.30–2.33).

Comparison of the relationships suggested by each analysis shows that the molecular and the morphological signals are conflicting. For example, the morphology-only analysis (Fig. 2.33) supports a monophyletic Theaceae s.l. (except *Sladenia*) with the Ternstroemioideae nested within a paraphyletic Theaceae s.s. (Camellioideae), while the analyses including molecular data support two clades, Theaceae s.s. and Ternstroemiaceae, which are not sister taxa (Figs. 2.30–2.32). Also, the morphology-only analysis places the Bonnetiaceae-Kielmeyeroideae within the "Ericales" clade (Fig. 2.33), while the analyses with molecular data included place them as sister to the asterid clade (Cornales + Ericales) (Figs. 2.30–2.32). This highlights the high level of homoplasy present in this group and in this floral plan. However, the conflict also exists among molecular partitions; the analysis with morphology + chloroplast regions (Fig. 2.32) shows more resolution than the total evidence or the morphology + organelle regions (Figs. 2.30, 2.31) suggesting that *matR* conflicts with *rbcL*, *matK*, and *trnL-F*. ITS on the other hand, provides resolution at the higher levels of the tree and does not conflict with deep nodes, perhaps because the ITS alignment was very difficult among distantly related members and many large gaps had to be added.

In conclusion, based solely on the structure of the consensus trees in our phylogenetic analyses, *Pentapetalum* would be an early member of the Ericales sensu APG (2003; Figs. 2.30, 2.31, 2.33) with pentaphylacacean affinities (sensu Schönenberger et al., 2005; Fig. 2.32)

In addition to *Pentapetalum*, the Old Crossman Clay Pit has produced an important number of fossil flowers belonging to the Ericales sensu APG (2003) with diverse floral morphologies (see Crepet, 1996, 2008) and different degrees of floral specialization. Many ericalean taxa illustrated in Crepet (1996 , 2008) show that by the Turonian, the Ericales clade had already diversified extensively and that some of its members had already evolved many advanced characters associated with insect pollination (e.g., clawed petals, inverted anthers, viscin threads, nectar). *Paleoenkianthus sayrevillensis* (Nixon and Crepet, 1993), for example, is a member of the Ericaceae whose anther morphology, anther dehiscence, and pollen grains show advanced adaptations to bee pollinators (Nixon and Crepet, 1993; Crepet, 1996, 2008). In contrast, *Pentapetalum* retains a basic floral plan that indicates little specificity toward pollinators; the actinomorphic, showy corolla, high number of stamens, and lack of evidence of nectar-producing structures point toward a nonspecific insect pollination syndrome with pollen as a reward.

Similar fossil evidence from the Åsen locality in southern Sweden of Late Santonian-Early Campanian age (Friis, 1984, 1985; Schönenberger and Friis, 2001) indicates that flowers with general ericalean and more specifically thealean features were also diverse in slightly younger sediments. *Paradinandra suecica* (Schönenberger and Friis, 2001), a taxon with entomophilous floral morphology was compared to the Ternstroemiaceae/Pentaphylacaceae, the same group to which *Pentapetalum* shows affinities. However the characters of *Paradinandra* and *Pentapetalum* point to very different strategies; while *Pentapetalum* probably offered pollen as a reward in an open corolla, *Paradinandra* seems to have produced nectar at the bottom of a salverform, sympetalous corolla (Schönenberger and Friis, 2001). If indeed, these two taxa belong to the Ternstroemiaceae/Pentaphylacaceae lineage, their

contrasting morphologies at such early stages in asterid evolution are an indication of the rapid and extensive diversification that the Ericales and more specifically the Ternstroemiaceae/Pentaphylacaceae lineage had undergone by the early Late Cretaceous.

In addition to the Old Crossman Pit in New Jersey and the Åsen locality in southern Sweden, other Late Cretaceous localities have produced a plethora of ericalean taxa. The Allon flora of Late Santonian age from central Georgia has produced a member of the Actinidiaceae confirmed by phylogenetic analysis, *Parasaurauia allonensis* (Keller et al., 1996), in addition to at least three "general ericalean " taxa (Herendeen et al., 1999). Similarly, a couple of ericalean taxa have been found in the Lower Coniacian flora of the Kamikitaba locality in northeastern Japan (Takahashi et al., 1999).

The evidence from an abundant and phylogenetically diverse ericalean fossil record well established by the early Late Cretaceous, in addition to evidence from molecular dating estimates (Bremer et al., 2004), supports the notion of an Early Cretaceous radiation of ericalean groups (Schönenberger et al., 2005). An Early Cretaceous diversification of the Ericales sensu APG (2003) would allow the establishment of lineages leading to modern families by the Late Cretaceous. *Pentapetalum* is another example of this Late Cretaceous ericalean diversity. However, although it can unequivocally be placed in the Ericales sensu APG (2003), and it can be shown to have thealean/ternstroemialean/pentaphylacacean affinities within the Ericales, it cannot be decisively assigned to a modern family. At the same time, it is very clear that it represents a taxon different from other fossils of similar age and " general thealean " affinities (i.e., *Paradinandra suecica* [Schönenberger and

Friis, 2001]). More comprehensive studies of these fossils in a phylogenetic context are needed to clarify the relationships of these fossils with each other and with extant members of the Ericales. However, for these analyses to be successful, the phylogenetic relationships of extant Ericales need to be more completely understood than they are at the present time.

APPENDIX

Taxa and GenBank accessions of sequences used in this study with appropriate references. Two or more accessions for the same molecular marker are separated by "/".

Taxon Accessions (Reference): *matK*, *rbcL*, *trnL-F*, *matR*, ITS.

Actinidia arguta ——, ——, AY156914 (Jung et al., 2003), AF420991 (Anderberg et al, 2002), ——. ***Actinidia chinensis*** U61324 (Prince and Parks, 2001), L01882 (Prince and Parks, 2001), AF543452 (Jung et al., 2003), ——, ——. ***Actinidia deliciosa*** ——, ——, AY156916 (Jung et al., 2003), ——, ——. ***Actinidia eriantha*** ——, ——, AF543454 (Jung et al., 2003), ——, ——. ***Actinidia hemsleyana*** ——, ——, AY156911 (Jung et al., 2003), ——, ——. ***Actinidia kolomikta*** AJ429279 (Bremer et al., 2002), ——, AY156912 / AJ430869 (Jung et al., 2003 / Bremer et al., 2002), ——, ——. ***Actinidia macrosperma*** ——, ——, AY156913 (Jung et al., 2003), ——, ——. ***Actinidia melanandra*** ——, ——, AF543453 (Jung et al., 2003), ——, ——. ***Actinidia polygama*** ——, ——, AY156915 (Jung et al., 2003), ——, ——. ***Actinidia rubricaulis*** ——, ——, ——, AY163745 (Yang et al., 2006), ——. ***Actinidia rufa*** ——, ——, AY156917 (Jung et al., 2003), ——, ——. ***Adinandra dumosa*** ——, Z83149 (Prince and Parks, 2001), ——, ——, ——. ***Adinandra hainanensis*** ——, ——, ——, ——, AF456255 (Yang et al., 2004). ***Adinandra hirta*** ——, ——, AF534657 (Yang et al., 2004), AY163739 (Yang et al., 2004), ——. ***Adinandra millettii*** AF380069 (Prince and Parks, 2001), ——, ——, ——, ——. ***Anneslea fragrans*** AF380070 (Prince and Parks, 2001), AF380032 (Prince and Parks, 2001), AF534658 (Yang et al., 2004), AY163734 (Yang et al., 2004), AY096024 (Yang et al., 2004). ***Apterosperma oblata*** AF380071 (Prince

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—, ——, ——. ***Clethra delavayi*** ——, ——, ——, AY163746 (Yang et al., 2006), ——. ***Cleyera japonica*** AF380078 (Prince and Parks, 2001), AF380038 (Prince and Parks, 2001), ——, ——, ——. ***Cleyera pachyphylla*** ——, ——, AF534664 (Yang et al., 2004), AY163737 (Yang et al., 2004), AY096025 (Yang et al., 2004). ***Cliftonia monophylla*** AF380079 (Prince and Parks, 2001), Z83140 (Prince and Parks, 2001), ——, ——, ——. ***Cornus canadensis*** U96890 (Xiang et al., 2005), L01898 (Xiang et al., 2005), ——, ——, AY530913 (Xiang et al., 2005). ***Cornus mas*** AJ429275 (Bremer et al., 2002), L11216 (Bremer et al., 2002), AJ430866 (Bremer et al., 2002), ——, AY530920 (Xiang et al., 2005). ***Cornus sericea*** ——, ——, ——, AY725883 (Schönenberger et al., 2005), ——. ***Cornus suecica*** ——, ——, ——, AF420990 (Anderberg et al, 2002), ——. ***Cyrilla racemiflora*** AF380080 (Prince and Parks, 2001), L01900 (Prince and Parks, 2001), ——, ——, ——. ***Eurya alata*** ——, AF380039 (Prince and Parks, 2001), ——, ——, AF456259 (Yang et al., 2004). ***Eurya handel -mazzettii***——, ——, AF534667 (Yang et al., 2004), AY163748 (Yang et al., 2004), ——. ***Eurya japonica*** AF380081 (Prince and Parks, 2001), ——, ——, ——, ——. ***Euryodendron excelsum*** ——, ——, AF534668 (Yang et al., 2004), AY163733 (Yang et al., 2004), AF456260 (Yang et al., 2004). ***Ficalhoa laurifolia*** ——, AF421109 (Anderberg et al, 2002), ——, AF421037 (Anderberg et al, 2002), ——–. ***Fouquieria splendens*** U96903 (Prince and Parks, 2001), L11675 (Prince and Parks, 2001), ——, ——, ——. ***Franklinia alatamaha*** AF380082 (Prince and Parks, 2001), AF380040 (Prince and Parks, 2001), AF534671 (Yang et al., 2004), AY163731 (Yang et al., 2004), AY096016 (Yang et al., 2004). ***Glyptocarpa camellioides*** AF380083 (Prince and Parks, 2001), AF380041 (Prince and Parks, 2001), ——, ——, ——. ***Gordonia brandegeei*** AF380084 (Prince and Parks, 2001), ——, ——, ——, ——. ***Gordonia lasianthus*** AF380085 (Prince and Parks, 2001), AF380042 (Prince and Parks, 2001), AY214936 (Yang et al., 2004), AY163735

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AY625031/ AY625033 (Notis, 2004), AY625009 (Notis, 2004), ——, ——, AY625618 / AY625619 (Notis, 2004). ***Marila plumbaginea*** ——, ——, ——, ——, AY625617 (Notis, 2004). ***Marila racemosa*** ——, AF518398 / AY625008 (Gustafsson et al., 2002 / Notis, 2004), ——, ——, AY625615 (Notis, 2004). ***Marila sp*** ——, ——, ——, ——, AY625616 (Notis, 2004). ***Marila tomentosa*** AY625032 (Notis, 2004), AY625010 (Notis, 2004), ——, ——, AY625620 (Notis, 2004). ***Parapyrenaria multisepala*** ——, ——, AY216568 (Yang et al., 2004), AY163742 (Yang et al., 2004), AF456263 (Yang et al., 2004). ***Pelliciera rhizophorae*** AJ429303 (Bremer et al., 2002), AF421099 / AJ428893 / AF206804 (Anderberg et al, 2002 / Bremer et al., 2002 / Soltis et al., 2000), AJ430891 (Bremer et al., 2002), AF421022 (Anderberg et al, 2002), ——. ***Pelliciera sp*** ——, ——, ——, ——, AY348856 (Yuan et al., 2004). ***Pentamerista neotropica*** ——, AY725860 (Schönenberger et al., 2005), ——, AY725886 (Schönenberger et al., 2005), ——. ***Pentaphylax euryoides*** AJ429291 (Bremer et al., 2002), AF419239 / AJ402986 / AJ428891 (Anderberg et al, 2002 / Savolainen et al., 2000 / Bremer et al., 2002), AJ430881 (Bremer et al., 2002), AY163749 / AF419243 (Yang et al., 2006 / Anderberg et al, 2002), ——. ***Physena sp*** ——, Y13116 (Morton et al., 1997), ——, ——, ——. ***Polyspora axillaris*** AF380090 (Prince and Parks, 2001), AF380047 (Prince and Parks, 2001), AY214937 (Yang et al., 2004), ——, AY214930 (Yang et al., 2004). ***Polyspora chrysandra*** AF380091 (Prince and Parks, 2001), AF380048 (Prince and Parks, 2001), AF534678 (Yang et al., 2004), AY163741 (Yang et al., 2004), AY214931 (Yang et al., 2004). ***Polyspora hainanensis*** AF380092 (Prince and Parks, 2001), AF380049 (Prince and Parks, 2001), AY216566 (Yang et al., 2004), ——, AY214932 (Yang et al., 2004). ***Polyspora kwangsiensis*** AF380093 (Prince and Parks, 2001), AF380050 (Prince and Parks, 2001), ——, ——, ——. ***Polyspora longicarpa*** ——, ——, AY214938 (Yang et al., 2004), ——, AF456264 (Yang et al., 2004). ***Polyspora tonkinensis*** ——, ——,

AY216563 (Yang et al., 2004), AY163728 (Yang et al., 2004), AY214933 (Yang et al., 2004). ***Polyspora yunnanensis*** AF380095 (Prince and Parks, 2001), AF380052 (Prince and Parks, 2001), ——, ——, ——. ***Pyrenaria shinkoensis*** AF380113 (Prince and Parks, 2001), AF380068 (Prince and Parks, 2001), ——, ——, ——. ***Pyrenaria yunnanensis*** ——, ——, ——, AY163730 (Yang et al., 2004), AF456270 (Yang et al., 2004). ***Rhododendron hippophaeoides*** U61353 (Prince and Parks, 2001), L01949 (Prince and Parks, 2001), ——, ——, ——. ***Sarracenia flava*** ——, L01952 (Prince and Parks, 2001), ——, ——, ——. ***Sarracenia purpurea*** U96906 (Prince and Parks, 2001), ——, ——, ——, ——. ***Schima argentea*** AF380096 (Prince and Parks, 2001), AF380053 (Prince and Parks, 2001), ——, ——, ——. ***Schima khasiana*** ——, ——, AF534680 (Yang et al., 2004), AY163740 (Yang et al., 2004), AF456269 (Yang et al., 2004). ***Schima noronhae*** AF380097 (Prince and Parks, 2001), AF380054 (Prince and Parks, 2001), ——, ——, ——. ***Schima remotiserrata*** AF380098 (Prince and Parks, 2001), AF380055 (Prince and Parks, 2001), ——, ——, ——. ***Schima superba*** AF380099 (Prince and Parks, 2001), ——, ——, ——, AF354641 (Yang et al., 2004). ***Schima wallichii*** AF380100 (Prince and Parks, 2001), AF380056 (Prince and Parks, 2001), ——, ——, ——. ***Sladenia celastrifolia*** AJ429297 (Bremer et al., 2002), AJ403004 / AF421108 (Savolainen et al., 2000 / Anderberg et al, 2002), AJ430081 (Bremer et al., 2002), AY163752 (Yang et al., 2006), ——. ***Stewartia gemmata*** ——, ——, AY216565 (Yang et al., 2004), AY163732 (Yang et al., 2004), ——. ***Stewartia malacodendron*** AF380101 (Prince and Parks, 2001), AF380057 (Prince and Parks, 2001), ——, ——, ——. ***Stewartia monadelpha*** AF380102 (Prince and Parks, 2001), AF380058 (Prince and Parks, 2001), ——, ——, ——. ***Stewartia ovata*** AF380103 (Prince and Parks, 2001), ——, AY216564 (Yang et al., 2004), ——, AF339861 (Yang et al., 2004). ***Stewartia pseudocamellia*** AF380104 (Prince and Parks, 2001), AF380059 (Prince and Parks,

2001), ——, ——, AF339863 (Yang et al., 2004). ***Stewartia rostrata*** ——, ——, ——, ——, AF456271 (Yang et al., 2004). ***Stewartia serrata*** AF380105 (Prince and Parks, 2001), AF380060 (Prince and Parks, 2001), ——, AY163736 (Yang et al., 2004), ——. ***Stewartia sinensis*** AF380106 (Prince and Parks, 2001), AF380061 (Prince and Parks, 2001), ——, ——, ——. ***Symplocos hookeri*** ——, ——, ——, AY163753 (Yang et al., 2006), ——. ***Symplocos paniculata*** ——, L12624 (Prince and Parks, 2001), ——, ——, ——. ***Symplocos sp*** AF380107 (Prince and Parks, 2001), AF380062 (Prince and Parks, 2001), ——, ——, ——. ***Symplocos tinctoria*** AF380108 (Prince and Parks, 2001), AF380063 (Prince and Parks, 2001), ——, ——, ——. ***Ternstroemia gymnanthera*** AF380109 (Prince and Parks, 2001), AF380064 (Prince and Parks, 2001), AF534683 (Yang et al., 2004), AY163754 (Yang et al., 2004), AF456272 (Yang et al., 2004). ***Ternstroemia longipes*** AF380110 (Prince and Parks, 2001), AF380065 (Prince and Parks, 2001), ——, ——, ——. ***Tetramerista sp*** AJ429304 (Bremer et al., 2002), Z80199 (Prince and Parks, 2001), AJ430892 (Bremer et al., 2002), ——, AY348858 (Yuan et al., 2004). ***Tutcheria championi*** AF380111 (Prince and Parks, 2001), AF380066 (Prince and Parks, 2001), ——, ——, ——. ***Tutcheria hirta*** AF380112 (Prince and Parks, 2001), AF380067 (Prince and Parks, 2001), ——, ——, ——. ***Tutcheria spectabilis*** ——, ——, AY216569 (Yang et al., 2004), AY163743 (Yang et al., 2004), AF456280 (Yang et al., 2004).

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CHAPTER 3

A REVISION OF THE GENUS *SOLANITES* WITH NOTES ON OTHER FOSSILS ASSIGNED TO SOLANACEAE

INTRODUCTION

The Solanaceae is a large cosmopolitan family of some 92-100 genera and 2300-2500 species (Olmstead et al., 1999, 2008; Hunziker, 2001; Martins and Barkman, 2005). The great diversity found within the family makes it difficult to find morphological characters that define it but in general, these are plants that produce alkaloids, they have hairs and frequently spines, the flowers have five sepals, five petals fused into a sympetalous corolla with five epipetalous stamens (sometimes reduced to four or two), the ovary is superior, syncarpic, of two obliquely oriented carpels with one style and a bilobed stigma (Cronquist, 1981; Tétény, 1987; Takhtajan, 1997). The family has been long recognized for its medicinal and toxic properties (i.e. *Datura*-jimsonweed, *Atropa*-belladonna or deadly nightshade, *Mandragora*-mandrake, *Nicotiana*-tobacco), agricultural products (i.e. *Solanum*-tomato, potato, eggplant, *Physalis*-tomatillo, *Capsicum*-chili peppers) and ornamental uses (i.e. *Petunia*-petunias, *Datura*-nightshade). For these reasons, the strong interest in studying this family continues to this day.

Despite the size of the family, its fossil record is very sparse for a number of reasons including, undersampling in the Neotropics where the greatest diversity is found, and preservational bias against herbaceous, non-deciduous plants. The paucity of fossils assignable to the Solanaceae has prevented the establishment of a reliably

calibrated timeline for its diversification. Thus, a review of the actual affinities of fossils that have been assigned to Solanaceae would be helpful in establishing an accurate temporal framework for other evolutionary studies in the family.

Of the eleven fossil species described as Solanaceae (Table 3.1), five are represented by flowers of the same fossil genus; *Solanites*. Four of them are also potentially the earliest members of the family. For these reasons a revision of the taxonomic status of that genus and of the species assigned to it is in order.

Table 3.1. Fossils assigned to Solanaceae.

Fossil taxon	Age	Locality	Reference
Flowers			
Solanites brongniartii Saporta 1862	Oligocene	Aix-en-Provence, France	Saporta, 1862
Solanites saportanus Berry 1916	Early Eocene	Claiborne, TN, USA	Berry, 1916
Solanites pusillus Berry 1930	Early Eocene	Claiborne, TN, USA	Berry, 1930
Solanites sarachaformis Berry 1930	Early Eocene	Claiborne, TN, USA	Berry, 1930
Solanites crassus Berry 1930	Early Eocene	Claiborne, TN, USA	Berry, 1930
Fruits			
Cantisolanum daturoides Reid et Chandler 1933	Early Eocene	London clay, England	Reid and Chandler, 1933
Physalis pliocaenica Szafer 1947	Late Miocene (Tortonian)	Stare Gliwice, Poland	Szafer, 1961
Seeds			
Solanispermum reniforme Chandler 1957	Eocene	Lower Bagshot, UK	Chandler, 1962
Solanum arnense Chandler 1962	Eocene	Lower Bagshot, UK	Chandler, 1962
Pollen			
Datura cf. *D. discolor* Leopold and Clay-Poole 2001	Late Eocene	Florissant, CO, USA	Leopold and Clay-Poole, 2001
Leaves			
Solandra haeliadum Massalongo 1851	Eocene	Salcedo, Italy	Massalongo, 1851

METHODS

LITERATURE REVIEW

Based on the revision of the fossil record of the Asteridae by Martinez-Millan (2010, this volume), eleven fossil taxa assigned to Solanaceae had been identified (Table 3.1). Of these eleven, those reported from the earliest deposits, the Early Eocene, were selected for further investigation. These fossil taxa are: *Solanites saportanus, S. sarachaformis, S. crassus, S. pusillus* and *Cantisolanum daturoides*.

The protologues of these fossil taxa were revised and the type specimens located in their housing institutions. In the case of the four [presumably] Early Eocene species of *Solanites*, it was necessary to not only locate their type specimens, but also to locate the type specimen of type species for the genus, *Solanites brongniartii* from the Oligocene, in order to evaluate their identifications. On the other hand, *Cantisolanum* is a monotypic genus known from only one locality, therefore, only one type specimen needed to be located.

DIRECT EXAMINATION

The type specimens of the five species of *Solanites* were observed in their housing institutions: The Muséum National d'Histoire Naturelle (MNHN) in Paris, France for *S. brongniartii* and the Smithsonian Institution National Museum of Natural History (USNM) in Washington, DC for the remaining species. Some additional specimens from North American localities were obtained on loan from the Florida Museum of Natural History (FMNH) and the University of Connecticut (UCPC). The specimens were studied by direct observation using mainly stereoscopic microscopes at the corresponding institutions and at the Paleobotanical Laboratory, Department of Plant Biology, Cornell University (Zeiss SV-11). Anthers or portions

of anthers of four specimens (UF15737-49566, UF15737-49567, UF15738-8214 and UCPC-P10) were removed from the fossil, mounted on an SEM stubs, sputter coated with gold/palladium and observed under a field emission Hitachi 4500 Scanning Electron Microscope at the Cornell Center for Materials Research. The stubs are kept at the Cornell University Paleobotanical Collection (CUPC-1724, CUPC-1725, CUPC-1727 to CUPC-1732 and CUPC-1734). Digital pictures were taken of all specimens. A few archived pictures taken by William Crepet and Charles Daghlian including the picture of a pollen grain taken on a compound microscope were scanned.

The type specimen of *Cantisolanum daturoides* was observed in its housing institution, the Natural History Museum in London, UK.

CLADISTIC ANALYSIS

Two of the fossil species (*S. brongniartii* and *S. pusillus*) had enough information for cladistic analyses to be performed.

***Analysis with* S. brongniartii**— A combined morphological and molecular matrix was compiled. For the molecular data, the six cpDNA sequences used by Bremer et al. (2002) –*rbcL*, *ndhF*, *matK*, *rps16*, *trnT-trnF*, and *trnV*– were downloaded from GenBank, aligned with CLUSTAL_X (Thompson et al., 1997) using a gap-opening penalty of 20.00 and a gap-extension penalty of 5.00, and manually adjusted afterward. A few corrections had to be made to the downloaded data before the alignment could be completed: (1)accession number AJ429683 (*trnV*) identified in GenBank with the name *Dipentodon sinicus* was changed to *Sanango sp.* in accordance with the table provided by Bremer et al. (2002), (2)the two accession

numbers AF130223 and AJ238344 reported in Bremer et al. (2002) as *rbcL* sequences were moved to the *ndhF* matrix as they correspond to that gene, (3)the inverse (reversed complement) sequence for accession number Z00044 (*Nicotiana tabacum* chloroplast genome) was used for the *rps16* sequence, (4)accession number U73971 for *Orobanche racemosa* was not used because Bremer et al. (2002) indicated it represents a pseudogene. After alignment, 5 leading positions from *matK*, 22 from *ndhF*, 22 trailing positions from *matK*, and 50 from *trnT-trnF* were removed as they were present in only one or two taxa. Conversely, 272 trailing positions from *ndhF* were trimmed because they were not confidently aligned. The *rbcL*, *rps16* and *trnV* matrices were not modified. Each of the six genes was subjected to the simple indel-coding method of Simmons and Ochoterena (2000) as implemented in the program GapCoder (Young and Healy, 2003). These six marker and six indel matrices were combined into a "molecular only" matrix of 132 taxa and 15147 characters (6899 informative) which is, in principle, equivalent to the Bremer et al. (2002) matrix. This matrix was analyzed to corroborate the Bremer et al. (2002) results using the same parameters and search strategies as for the combined "total evidence" matrix (see below).

A morphological matrix (Table 3.2) based on the taxa used by Bremer et al. (2002) was constructed using family descriptions by Cronquist (1981) and Takhtajan (1997) and digital photographs available at www.plantsystematics.org. The matrix has 111 taxa and 23 characters:

1. Flower sexuality: bisexual = 0; unisexual = 1.
2. Flower size (considered as corolla diameter): less than 1 cm = 0; more than 1 cm = 1.
3. Corolla symmetry: actinomorphic = 0; zygomorphic = 1.

4. Corolla shape [additive]: narrow: salverform / tubular = 0; widening: campanulate / urceolate / infundibiliform = 1; open: rotate (flat) / reflexed / lobed = 2.
5. Corolla aestivation: valvate = 0; convolute / contorte = 1; imbricate / quincuncial = 2.
6. Corolla merosity: trimerous = 0; tetramerous = 1; pentamerous = 2; hexamerous = 3; octamerous = 4.
7. Corolla fusion [additive]: free petals (polypetalous) = 0; fused at the base (basally gamopetalous) = 1; fused with lobes (gamopetalous) = 2; fully fused, no lobes (gamopetalous) = 3; fused distally (calyptra) = 4.
8. Corolla texture: membranaceous = 0; coriaceous = 1.
9. Corolla persistence: persistent = 0; caducous / deciduous = 1.
10. Petal midvein: absent = 0; present = 1.
11. Apices of petals: straight = 0; tortuous = 1; involute = 2; revolute = 3.
12. Stamen number relative to petals: haplostemonous = 0; diplostemonous = 1; anisomerous (less than petals) = 2; numerous = 3.
13. Stamen cycle orientation: alternate with petals (alternipetalous) = 0; opposite to petals (antepetalous) = 1; centrifugal / centripetal = 2.
14. Stamen attachment: to gynoecium = 0; to petals (epipetalous) = 1; to receptacle = 2.
15. Filament vs. anther: short = 0; long = 1.
16. Anther surface: striated = 0.
17. Connective projection: absent = 0; present = 1.
18. Anther dehiscence: longitudinal slits = 0; poricidal = 1.
19. Stamens vs. corolla lobes (non flat corolla): exserted = 0; included = 1.
20. Carpel number: 2 = 1; 3 = 2; 4 = 3; 5 = 4; more than 5 = 5.

21. Ovary: apocarpous = 0; syncarpous = 1.
22. Number of styles: 0 = 0; 1 = 1; 2 = 2; 3 = 3; 4 = 4; 5 = 5; more than 5 = 6.
23. Stigma shape: simple = 0; capitate = 1; clavate = 2; lobed (carpel number) = 3; lingulate = 4.

The final, total evidence matrix has 133 taxa and 15170 characters of which 6920 are informative (Table 3.3). Four different sets of analyses were performed based on this matrix. The first, "total evidence", includes all the characters and taxa. The matrix was analyzed 10 times using TNT (Goloboff et al., 2003, 2008). Each analysis consisted in 1000 replications of subtree pruning and regrafting (SPR) on randomly generated Wagner trees holding up to 10 trees per replication, followed by a round of tree bisection-reconnection (TBR) (rseed 0; mult= spr replic 1000 hold 10; bbreak=tbr). Standard bootstrap values were calculated on 1000 TBR replications of 5 runs each, holding up to 5 trees per replication and keeping the consensus only.

The second, "without gynoecium characters" uses the same matrix and the same parameters as the first analysis but the character state for characters 20 (carpel number), 22 (style number), and 23 (stigma shape) in *Solanites brongniartii* has been changed to "?" in order to test the interpretation of the gynoecium in the fossil.

The third, "without fossil", excludes the taxon *Solanites brongniartii*. Its objective is to determine the effect of the fossil in the strict consensus. This matrix has 132 taxa and 15170 characters of which 6920. The analysis used the same parameters as the "total evidence" analysis.

The fourth, “character-by-character”, used the total evidence matrix with one morphological character turned off. Two morphological characters, 16-anther surface and 21-ovary, were excluded from all the analyses because they are uninformative. The remaining 21 characters were turned off one-at-a-time and one run of 1000 SPR replications holding up to 10 trees per replication followed by a round of TBR (rseed 0; mult= spr replic 1000 hold 10; bbreak=tbr) was performed in each case.

The resulting trees were evaluated in Winclada version 1.00.08 (Nixon, 2002) where strict consensuses were constructed for each analysis.

Table 3.2. Matrix of morphological characters including the fossil taxon, *Solanites brongniartii*. A-[234], B-[12345], C-[23456], D-[01], E-[12], F-[02], G-[2345], H-[345], I-[124], J-[123], K-[012], L-[013], M-[13], N-[01234], O-[014], P-[123456], Q-[34], R-[03], S-[23], T-[45], U-[1234], V-[0123], W-[14], X-[24], Y-[15].

Character	1	5	10	15	20
Paeoniaceae *Paeonia*	0 1 0 2 - A 0 0 ? 0 0 3 2 2 1 ? 0 0 - B 0 C 1
Vitaceae *Vitis*	0 0 0 - 0 2 0 1 1 0 - 0 1 2 1 ? 0 0 - 1 1 1 1
Acanthaceae *Avicennia* Lamiales	0 0 D E 2 1 1 ? ? 0 0 0 0 1 1 ? 0 0 0 1 1 1 3
Acanthaceae *Acanthus* Lamiales	0 1 D F E 2 2 ? ? ? 0 2 0 1 1 ? ? 0 1 1 1 1 3
Actinidiaceae *Actinidia* Ericales	D 1 0 2 2 2 D 0 ? 0 0 3 E 1 1 ? 0 D - G 1 H 0
Adoxaceae *Viburnum* Dipsacales	0 0 D F F 2 2 ? ? 0 3 0 0 1 1 ? 0 0 0 I 1 1 1
Alseuosmiaceae *Alseuosmia* Asterales	D 1 0 0 0 J 2 ? ? 0 0 0 0 E 1 ? 0 0 0 1 1 1 3
Apiaceae *Apium* Apiales	D 0 D 2 0 2 0 0 ? 0 2 0 0 2 1 ? 0 0 - 1 1 2 0
Apocynaceae *Alstonia* Gentianales	0 1 0 D K E 2 ? ? ? L 0 0 1 0 ? ? 0 1 1 1 E 1
Aquifoliaceae *Ilex* Aquifoliales	1 0 0 2 F 1 1 1 0 0 F 0 0 1 1 ? ? 0 - H 1 D M
Araliaceae *Aralia* Apiales	D 0 0 2 F N O 1 1 0 0 0 0 2 1 ? 0 0 - B 1 P 0
Aralidiaceae *Aralidium* Apiales	1 ? 0 2 2 2 0 ? ? 0 0 0 0 2 1 ? 0 0 - 2 1 3 0
Argophyllaceae *Argophyllum* Asterales	0 ? 0 2 0 2 1 1 ? 0 ? 0 0 2 1 ? 0 0 - ? 1 1 M
Asteraceae *Helianthus* Asterales	D D D F 0 2 2 0 0 0 0 0 0 1 0 ? 1 0 1 1 1 1 3
Balsaminaceae *Impatiens* Ericales	0 0 1 0 - 2 2 0 ? ? 0 0 - 2 0 ? 0 ? 1 Q 1 1 0
Bignoniaceae *Jacaranda* Lamiales	0 1 1 0 F 2 2 ? ? ? 0 R 2 0 1 1 ? ? 0 1 1 1 1 3
Boraginaceae *Borago*	0 D 0 D K J 2 ? ? 0 0 0 0 1 0 ? ? 0 1 1 1 1 3
Boraginaceae *Pholisma*	0 0 0 1 ? A S ? ? 0 0 0 ? 1 0 ? 0 0 1 T 1 1 M
Bruniaceae *Brunia*	0 0 0 2 2 E 1 ? ? ? 0 0 0 E 1 ? D 0 - E 1 J 0
Byblidaceae *Byblis* Lamiales	0 ? 0 2 1 2 1 0 ? ? 0 0 0 E 0 ? 0 1 - 1 1 1 1
Calyceraceae *Boopis* Asterales	0 ? D 0 0 J 2 ? ? 0 0 0 0 1 1 ? 0 0 ? 1 1 1 1
Campanulaceae *Campanula* Asterales	D 1 D D 0 2 2 ? ? 1 0 0 0 D 1 ? 0 0 0 I 1 1 3
Caprifoliaceae *Lonicera* Dipsacales	0 ? 1 F F 2 2 ? ? 1 0 0 0 1 1 ? 0 0 0 E 1 1 1
Cardiopteridaceae *Cardiopteris* Aquifoliales	D 0 0 0 2 2 1 ? ? ? 0 0 0 1 0 ? 0 0 ? 1 1 2 D
Clethraceae *Clethra* Ericales	0 0 0 2 2 S D 0 ? 0 2 1 D 2 1 ? 0 1 - 2 1 1 3
Columelliaceae *Columellia*	0 ? 1 2 2 I 1 ? 0 0 0 2 0 1 0 ? 0 0 - 1 1 1 3
Columelliaceae *Desfontainia*	0 1 0 0 E 2 2 1 ? 0 0 0 0 1 0 ? 0 0 1 4 1 1 1
Convolvulaceae *Ipomea* Solanales	D 1 0 1 D E 3 0 ? 1 0 0 0 1 1 ? ? 0 1 1 1 E 0
Cornaceae *Cornus* Cornales	D 0 0 F F E 0 ? ? ? 0 0 0 2 1 ? ? 0 0 U 1 1 M
Cyrillaceae *Cyrilla* Ericales	0 ? 0 2 E S D 1 ? 0 0 D 0 2 1 ? 0 0 - U 1 D R
Diapensiaceae *Diapensia* Ericales	0 ? 0 2 E 2 2 ? 1 1 0 1 0 1 1 ? 0 0 - 2 1 1 3
Dipentodontaceae *Dipentodon*	0 0 0 2 0 S 0 ? ? ? 0 0 0 2 1 ? 0 0 - 2 1 1 0
Dipsacaceae *Dipsacus* Dipsacales	0 ? D D 2 2 2 ? ? 1 0 2 0 1 1 ? 0 0 0 1 1 1 R
Ebenaceae *Diospyros* Ericales	0 1 0 2 K V 2 1 0 0 3 M 0 1 D ? 0 D - M 1 W 0
Ebenaceae *Lissocarpa* Ericales	0 ? 0 0 1 1 2 1 ? ? 0 1 D 1 0 ? 1 0 1 3 1 1 2
Eremosynaceae *Eremosyne*	0 0 0 2 0 2 0 ? ? ? 0 0 0 2 1 ? 0 0 - 1 1 2 1
Ericaceae *Erica* Ericales	0 0 0 1 E E K 0 ? 0 R 1 D 2 1 ? 0 1 1 Q 1 1 M
Escalloniaceae *Escallonia*	0 D 0 0 F E 0 0 0 1 R 0 0 2 1 ? 0 0 1 U 1 1 M
Eucommiaceae *Eucommia* Garryales	1 0 0 - - - - - - - - - - 2 0 ? 1 0 - 1 1 1 0
Fouqueriaceae *Fouqueria* Ericales	0 1 0 0 2 2 2 ? ? 0 0 M - 2 1 ? 0 0 0 2 1 M 0
Garryaceae *Aucuba* Garryales	1 ? 0 2 0 1 0 1 ? 0 0 0 0 2 1 ? 0 0 - ? ? 1 1
Garryaceae *Garrya* Garryales	1 0 0 - - 1 - - - - - 0 - 2 1 ? 0 0 0 E 1 S 0
Gelsemiaceae *Gelsemium* Gentianales	0 ? 0 1 2 2 2 0 ? 0 0 0 0 1 1 ? 0 0 1 1 1 1 0
Gentianaceae *Gentiana* Gentianales	D ? 0 ? 1 E 2 0 ? 1 0 0 0 1 1 ? 0 D ? 1 1 1 3
Gesneriaceae *Streptocarpus* Lamiales	0 1 1 0 2 2 2 ? ? ? 0 2 0 1 1 ? 0 0 0 1 1 1 3

Table 3.2. (Continued)

Character	1	5	10	15	20
Goodeniaceae *Scaevola* Asterales	0 ? 1 0 0 2 2 ? ? 1 0 0 0 D 1 ? ? 0 1 1 1 1 0
Griseliniaceae *Griselinia* Apiales	1 0 0 2 2 2 0 ? ? 1 0 0 0 2 1 ? 0 0 - 2 1 3 0
Grubbiaceae *Grubbia* Cornales	0 0 0 - - 1 - - - - - - 1 0 2 1 ? 1 0 - 1 1 1 3
Helwingiaceae *Helwingia* Aquifoliales	1 0 0 2 0 K 0 ? ? 1 0 0 0 2 1 ? 0 0 - S 1 Q 0
Hydrangeaceae *Hydrangea* Cornales	D 1 0 ? K E 0 ? ? 1 0 L K 2 1 ? 0 ? 0 B 1 C D
Icacinaceae *Icacina*	D ? 0 2 0 V K ? ? ? 0 0 0 E 1 ? ? 0 - U 1 1 3
Lamiaceae *Lamium* Lamiales	D ? 1 0 2 2 2 ? ? 0 0 2 0 1 1 ? ? 0 1 1 1 1 3
Lecythidaceae *Barringtonia* Ericales	0 1 1 2 2 J 0 1 1 0 0 3 2 2 1 ? 0 D - B 1 1 M
Lentibulariaceae *Pinguicula* Lamiales	0 0 1 0 2 2 2 ? ? 0 0 2 ? 1 1 ? 0 0 1 1 1 D 3
Loasaceae *Loasa* Cornales	0 1 0 2 0 2 K ? ? 0 2 M E E 1 ? 0 0 - G 1 1 0
Loganiaceae *Logania* Gentianales	0 ? 0 1 2 E 2 ? ? 1 0 0 0 1 1 ? 0 0 1 E 1 1 1
Maesaceae *Maesa* Ericales	0 0 0 0 ? 2 2 1 0 0 0 0 1 1 0 ? 0 0 0 1 1 1 3
Marcgraviaceae *Marcgravia* Ericales	0 ? 0 - - E O 1 1 0 - 3 - E 1 ? 0 0 - B 1 0 R
Martyniaceae *Proboscidea* Lamiales	0 1 1 1 2 2 2 0 ? 0 0 2 0 1 1 ? 0 0 1 1 1 1 3
Melanophyllaceae *Melanophylla* Apiales	0 ? 0 2 2 2 0 1 ? 0 2 0 0 2 0 ? 0 0 - E 1 S 0
Menyanthaceae *Menyanthes* Asterales	0 1 0 2 F 2 2 ? ? 0 0 0 0 1 1 ? ? 0 - 1 1 1 3
Montianiaceae *Kaliphora* Solanales	1 0 0 2 0 1 0 1 ? ? 3 0 0 2 0 ? 1 0 - 1 1 ? 0
Montianiaceae *Montinia* Solanales	1 0 0 2 2 K 0 1 1 ? 0 0 0 2 1 ? 0 0 - 1 1 1 M
Morinaceae *Morina* Dipsacales	? ? D 0 2 2 2 ? ? 1 0 2 ? 1 1 ? 0 0 0 1 1 1 R
Myrsinaceae *Myrsine* Ericales	0 0 0 F K 2 2 1 0 0 R 0 1 1 0 ? 0 D 0 A 1 1 L
Oleaceae *Olea* Lamiales	0 0 0 2 K 1 2 ? ? ? 0 F 0 1 0 ? 1 0 - 1 1 1 3
Oncothecaceae *Oncotheca*	0 0 0 1 2 2 2 ? ? ? ? 0 0 1 0 ? 1 0 ? 4 1 0 -
Orobanchaceae *Cyclocheilon* Lamiales	0 ? 1 1 2 2 2 0 ? 0 ? 2 0 1 1 ? 0 0 1 1 1 1 4
Orobanchaceae *Lindenbergia* Lamiales	0 1 1 0 2 2 2 ? ? 1 0 2 0 1 1 ? ? 0 1 1 1 1 M
Paracryphiaceae *Paracryphia*	D 0 0 2 2 2 0 ? 0 ? ? D D 2 1 ? 0 0 - U 1 G 1
Pedaliaceae *Sesamum* Lamiales	0 ? 1 0 2 2 2 ? ? ? 0 F 0 1 1 ? ? 0 1 1 1 1 3
Pentaphragmataceae *Pentaphragma* Asterales	D 0 0 2 0 2 E 1 ? ? 0 0 0 1 0 ? 0 0 - E 1 1 1
Pentaphylacaceae *Pentaphylax* Ericales	0 ? 0 2 2 2 0 ? ? 0 0 0 0 2 1 ? 0 1 - 4 1 1 3
Phellinaceae *Phelline* Asterales	1 ? 0 2 0 J 0 1 ? 0 2 0 0 2 0 ? 0 0 - U 1 0 3
Phrymaceae *Phryma* Lamiales	0 0 1 0 ? 2 2 0 ? ? 0 2 0 1 1 ? 0 0 1 1 1 1 3
Phyllonomaceae *Phyllonoma* Aquifoliales	0 0 0 2 0 E 0 0 ? ? 0 0 0 2 1 ? 0 0 - 1 1 2 0
Pittosporaceae *Pittosporum* Apiales	D 0 0 2 2 2 D ? ? 1 0 0 0 2 0 ? 0 D - 1 1 1 M
Plantaginaceae *Antirrhinum* Lamiales	0 1 1 0 F E 2 ? ? 1 0 F 0 1 1 ? 0 0 1 1 1 1 R
Plantaginaceae *Globularia* Lamiales	0 0 1 0 2 2 2 ? ? ? 0 F 0 1 1 ? ? 0 0 1 1 1 M
Plantaginaceae *Plantago* Lamiales	D 0 0 2 2 1 0 0 ? 1 0 0 ? 2 1 ? 0 0 - 1 1 1 3
Plocospermataceae *Plocosperma* Lamiales	1 ? 0 1 2 2 2 ? ? ? 0 0 0 1 1 ? 0 0 1 1 1 1 0
Polemoniaceae *Polemonium* Ericales	0 1 0 0 1 J 2 ? ? ? 0 0 0 1 1 ? ? 0 1 2 1 1 3
Primulaceae *Primula* Ericales	0 1 0 2 2 N 2 0 ? 0 0 0 1 1 0 ? 0 D - 4 1 1 1
Roridulaceae *Roridula* Ericales	0 ? 0 ? E 2 1 ? ? ? 0 0 0 1 1 ? 0 1 ? 2 1 1 M
Rousseaceae *Carpodetus* Asterales	0 0 0 2 0 S 0 0 1 ? 0 0 0 2 1 ? 0 0 - A 1 1 1
Rousseaceae *Roussea* Asterales	0 1 0 0 0 E 2 1 0 0 3 0 0 2 1 ? 0 0 0 T 1 1 1
Rubiaceae *Luculia* Gentianales	D 1 0 0 K E 2 ? ? ? 0 0 0 1 1 ? ? 0 1 I 1 1 M
Sapotaceae *Manilkara* Ericales	0 0 0 1 2 U 2 ? ? 0 F M 1 1 1 ? 0 0 0 B 1 1 M

Table 3.2. (Continued)

Character	1	5	10	15	20
Sarraceniaceae *Sarracenia* Ericales	0 1 0 2 2 2 0 ? 1 0 0 M 2 2 1 ? 0 0 - 4 1 1 3
Scrophulariaceae *Buddleja* Lamiales	0 ? 0 0 F E 2 ? ? 0 0 0 0 1 1 ? 0 0 1 1 1 1 M
Scrophulariaceae *Myoporum* Lamiales	0 ? D F 2 2 2 ? ? ? 0 F 0 1 1 ? 0 0 0 1 1 1 0
Scrophulariaceae *Scrophularia* Lamiales	0 1 1 F F 2 2 ? ? 1 0 F 0 1 1 ? 0 0 0 1 1 1 3
Solanaceae *Nicotiana* Solanales	0 1 0 K K E J ? ? ? R F 0 1 D ? ? D D 1 1 1 3
Sphenocleaceae *Sphenoclea* Solanales	0 0 0 1 2 2 2 0 1 ? 0 0 0 1 0 ? ? 0 1 1 1 0 1
Stilbaceae *Stilbe* Lamiales	0 ? 0 0 1 2 2 ? ? 0 0 0 0 1 0 ? 0 0 1 1 1 1 3
Stylidiaceae *Donatia* Asterales	0 ? 0 2 2 2 0 ? ? 0 0 2 ? 0 1 ? 0 0 ? E 1 S 1
Stylidiaceae *Stylidium* Asterales	0 ? 1 0 2 2 2 ? ? 0 0 2 ? 0 1 ? 0 0 0 1 1 1 3
Styracaceae *Styrax* Ericales	D ? 0 E F 2 K 0 ? 1 0 M 0 E 1 ? 1 0 D U 1 1 M
Symplocaceae *Symplocos* Ericales	D 1 0 E 2 N 1 1 ? 0 2 M 0 1 1 ? 0 0 0 U 1 1 M
Ternstroemiaceae *Ternstroemia* Ericales	0 1 0 2 2 2 0 0 ? 0 F M - 2 1 ? 0 0 - X 1 M 3
Tetrachondraceae *Tetrachondra* Lamiales	0 ? 0 2 2 1 2 ? ? ? 0 0 0 1 1 ? ? 0 - 1 1 1 1
Tetrameristaceae *Pelliciera* Ericales	0 1 0 2 2 2 0 ? 1 0 0 0 0 2 1 ? 1 0 - 1 1 1 0
Tetrameristaceae *Tetramerista* Ericales	0 ? 0 2 2 E 0 ? ? 0 ? 0 0 2 1 ? 0 0 - Q 1 1 R
Theaceae *Schima* Ericales	0 1 0 2 2 2 D 0 ? 0 0 M 1 E 1 ? D 0 - U 1 Y 3
Theophrastaceae *Theophrasta* Ericales	0 1 0 2 2 E 2 1 ? 0 0 0 1 1 1 ? 1 0 - 4 1 1 0
Torricelliaceae *Torricellia* Apiales	1 0 0 1 0 2 0 ? ? ? ? 0 0 2 ? ? 0 0 1 S 1 3 R
Tribelaceae *Tribeles*	0 0 0 1 1 2 0 1 ? ? ? 0 0 2 1 ? 0 0 ? 2 1 1 3
Vahliaceae *Vahlia*	0 0 0 2 2 2 0 ? ? ? 0 0 0 2 1 ? 0 0 - E 1 S 1
Valerianaceae *Valeriana* Dipsacales	D ? D D 2 K 2 ? ? 1 0 2 0 1 1 ? 0 0 0 2 1 1 R
Verbenaceae *Verbena* Lamiales	0 1 D D 2 I 2 ? ? 0 0 2 0 1 1 ? ? 0 1 1 1 1 3
Solanites brongniartii	0 0 0 2 0 2 E 0 1 1 1 0 0 1 0 0 1 ? - 1 ? 2 1

Table 3.3. Composition of the data matrix for the phylogenetic analysis of *Solanites brongniartii*. char-characters, inf-informative characters.

partition	# char	# inf	# taxa	partition	# char	# inf	# taxa
morphology	23	21	111	*matK* indels	471	141	131
matK	2194	1334	131[a]	*ndhF* indels	101	26	127
ndhF	2403	1248	127[b]	*rbcL* indels	7	1	131
rbcL	1432	493	131	*rps16* indels	766	308	125
rps16	1453	755	125	*trnT-F* indels	1054	297	129
trnT-F	2299	1103	129	*trnV* indels	733	261	125
trnV	2234	935	125	Total	15170	6920	133

[a]-two *Griselinia* and [b]-two *Ilex* sequences were combined in one for the final matrix.

***Analysis with* S. pusillus**— The aligned data matrix used by Richardson et al. (2000) was downloaded from the American Journal of Botany supplementary data site (http://ajbsupp.botany.org/v87/). This matrix includes 66 taxa (14 outgroups) and 2807 characters: 1428 *rbcL*, 1363 *trnL* and 16 representing *trnL* indels.

The morphological data matrix of Calvillo-Canadell (2000) which has 18 taxa and 26 characters was obtained from the author (Table 3.4). This matrix includes two outgroups, *Vitis* (Vitaceae) and *Mortonia* (Celastraceae) and two fossil flowers assigned to Rhamnaceae, *Nahinda axamilpensis* from the Oligocene and *Coahuilanthus belindae* from the Cretaceous (Calvillo-Canadell and Cevallos-Ferriz, 2007). The characters are:

1. Petal width (mm): 0.15 = 0; 0.30-0.60 = 1; 0.90+ = 2.
2. Petal length (mm): 0.50-0.90 = 1; 1.00-1.80 = 2; 3+ = 3.
3. Sepal width (mm): 0.30-0.70 = 1; 0.90-1.50 = 2; 2+ = 3.
4. Sepal length (mm): 0.70-1.10 = 0; 1.20-1.40 = 1; 1.50-1.80 = 2; 2+ = 3.
5. Ring diameter (mm) (insertion of other floral parts area): 0.70-1.10 = 0; 1.20-1.50 = 1; 2.00-2.10 = 2; 3+= 3.

6. Pedicel length (mm): 0.30-1.70 = 0; 2.00-3.00 = 1; 3.50-5.00 = 2.
7. Ovary length: 0.20-0.30 = 0; 0.40-0.60 = 1.
8. Flower length (mm): 1.50-3.90 = 0; 4.00-4.80 = 1; 5.00-6.81 = 2.
9. Claw in petal: absent = 0; short = 1; long = 2.
10. Petal shape: cucullate = 0; obovate = 1; ovate concave = 2; linear = 3; urceolate = 4; valvate = 5; imbricate = 6.
11. Petal apex: no emarginate = 0; emarginate = 1.
12. Sepal shape: triangular = 0; triangular deltate = 1; triangular reflexed = 2; triangular lobed = 3; triangular acute = 4; triangular ovate = 5; triangular inflexed = 6.
13. Keel: absent = 0; not prominent = 1; prominent = 2.
14. Enlarged sepal apex: absent = 0; present = 1.
15. Fruit type: drupe = 0; unilocular capsule = 1; trilocular capsule= 2; schizocarp = 3; berry = 4; samara = 5.
16. Fruit shape: globose = 0; subglobose = 1; obovoid = 2; elipsoid = 3; ovoid = 4.
17. Pyrene number: none = 0; two pyrene = 2; three pyrene = 3.
18. Locule number: two = 2; three = 3.
19. Petal presence: always present = 1; frequently present = 2; rarely present = 3.
20. Ovary type: inferior = 0; superior = 1; seminferior = 2; semisuperior = 3.
21. Floral cup shape: hemisphaeric = 0; campanulate = 1; obconic = 2; patelliform = 3; urceolate = 4.
22. Flower sex: perfect = 0; imperfect = 1; perfect y poligamous = 2.
23. Stamen size: longer than petals = 0; shorter than petals = 1; shorter than sepals = 2.

24. Floral part number: 4 or 6 = 0; 5 = 1; 4 or 5 = 2; 3 to 5 = 3.
25. Corolla vs. calyx: same size = 0; corolla bigger than calyx = 1; corolla smaller than calyx = 2.
26. Winged fruit: not winged = 0; winged = 1.

Table 3.4. Matrix of morphological characters including the fossil taxa, *Nahinda axamilpensis*, *Coahuilanthus belindae*, and *Solanites pusillus*. A-[01], K-Cretaceous, Olig-Oligocene, Eoc-Eocene.

Character	1				5					10					15					20					25		
Vitis	1	1	1	1	0	2	?	2	0	5	0	6	0	0	4	2	0	2	1	1	4	0	0	2	0	0
Mortonia	2	2	2	0	0	2	?	2	0	6	0	4	0	0	?	?	0	2	2	1	1	0	1	3	0	0
Adolphia	1	2	2	1	1	1	1	2	2	4	0	4	2	0	0	0	0	3	1	1	1	0	1	1	1	0
Berchemia	1	2	2	2	0	1	0	0	1	1	0	4	2	0	0	2	0	2	1	1	1	2	0	1	0	0
Ceanothus	2	2	2	1	0	2	0	1	2	0	0	5	1	0	1	0	3	3	1	2	2	0	0	1	1	0
Colletia	-	-	-	-	-	-	-	-	0	3	0	2	1	0	2	0	0	3	1	2	1	0	1	0	2	0
Colubrina	1	2	2	2	2	2	1	2	1	0	0	1	1	0	A	1	0	3	1	2	0	0	1	1	2	0
Condalia	-	-	2	1	2	0	0	0	0	-	0	1	1	0	0	4	0	2	3	1	0	0	2	1	-	0
Coahuilanthus (K)	1	1	1	0	0	0	0	0	1	-	0	4	1	0	-	-	-	-	3	3	1	1	-	1	2	0
Nahinda (Olig)	1	2	2	0	2	2	1	2	1	0	0	1	2	1	-	-	-	-	1	2	0	0	0	1	2	0
Gouania	1	1	1	0	1	1	1	1	1	0	0	3	1	0	3	-	0	3	1	0	2	2	1	1	2	1
Karwinskia	1	2	2	1	1	0	0	1	1	4	1	4	2	0	0	2	0	2	1	1	2	0	0	1	2	0
Krugiodendron	-	-	2	1	2	1	1	1	-	-	0	4	2	1	0	4	0	2	2	1	2	0	2	1	-	0
Paliurus	0	1	1	0	1	0	0	0	1	0	1	0	2	0	5	-	-	A	1	1	3	0	0	1	0	1
Reynosia	-	-	2	1	0	1	0	1	-	-	0	3	1	0	0	4	0	2	2	1	0	0	2	1	-	0
Rhamnus	1	1	2	2	0	2	1	2	1	2	1	4	1	0	0	2	3	2	2	1	1	2	1	2	1	0
Sageretia	0	2	1	0	1	0	0	0	1	0	0	4	2	0	0	3	2	3	1	1	3	0	0	1	2	0
Ziziphus	1	2	2	1	2	1	1	1	1	0	0	0	2	1	0	0	0	3	2	1	0	0	0	1	2	0
Solanites pusillus (Eoc)	2	3	3	3	3	?	?	-	0	1	0	0	1	1	?	?	?	?	1	?	0	0	-	1	?	?

The molecular matrix of Richardson et al. (2000) was reduced by fusing species of the same genus into one single taxon and deleting genera not present in the morphological matrix. In addition, five sequences were added to the matrix: (1)*trnL* sequence for *Adolphia infesta* (AY460408, Aagesen et al., 2005), (2)*trnL* sequence for *Vitis vinifera* (EF179097, Rossetto et al., 2007), (3)*rbcL* sequence for *V. aestivalis*

(L01960, Albert et al., 1992), (4)*trnL* sequence for *Mortonia greggii* (DQ217437, Islam et al., 2006), and (5)*rbcL* sequence for *M. greggii* (AY935727, Zhang and Simmons, 2006). The addition of the five sequences and the reduction in the number of taxa resulted in an alignment adjustment with a consequent change in the *trnL* indel presence/absence matrix. The new *trnL* indel matrix was reconstructed using the program GapCoder (Young and Healy, 2003). The final matrix has 19 taxa and 2751 characters (Table 3.5).

Table 3.5. Composition of the data matrix for the phylogenetic analysis of *Solanites pusillus*. char-characters, inf-informative characters.

partition	# characters	# informative	# taxa
morphology	26	25	19
rbcL	1428	107	16
trnL	1195	83	16
trnL indels	102	34	16

The matrix was analyzed using implicit enumeration on TNT (Goloboff et al., 2003, 2008). The resulting trees were evaluated in Winclada version 1.00.08 (Nixon, 2002) where the strict consensus was constructed. Standard bootstrap values were calculated on 1000 implicit enumeration replications on TNT keeping the consensus only.

RESULTS

EUROPEAN SOLANITES

Nomenclatural history— In 1855, Oswald Heer, then Director of the Zürich Botanical Garden published the first part of *Flora Tertiaria Helvetiae*, "The Tertiary Flora of Switzerland". The third part of the series, published in 1859, included an

appendix titled *Ueber das Klima und die Vegetationsverhältnisse des Tertiärlandes*, "On the climate and vegetation conditions of the Tertiary lands" (Heer, 1859a,b). This appendix compared the different Tertiary floras known at the time, especially those of Europe: Switzerland, Italy, Austria, Germany, Greece, Hungary, Romania, Russia, France, England and Iceland.

In 1861, Charles Th. Gaudin translated this appendix from German to French and published it as a separate book under the title *Recherches sur le climat et la Végétation du Pays Tertiaire*, "Investigations on the climate and the vegetation of the Tertiary" (Heer, 1861). In this version, the original 3-page-long section on France was replaced with some excerpts of the original text followed by a 55-page-long treaty on the Tertiary floras of Provence, written by the Count Louis Charles Joseph Gaston de Saporta and titled *Examen analytique des flores tertiaries de Provence, précédé d'une notice géologique et paléontologique sur les terrains tertiaires lacustres de cette région par M. Phil. Matheron*, "Analytical exam of the Tertiary floras of Provence, preceded by a geological and paleontological note on the lacustrine terrains of that region". In this treaty, Saporta provided an overview of the fossil flora of Aix-en-Provence and, in page 146 (30 of this section), he discussed some flowers pointing out "[One] specimen, in perfect state of conservation" and naming them *Solanum brongniarti* Sap [sic] after Brongniart suggested that "…[valvate aestivation] along with anther structure … is an indication of the probable assignation of these flowers to the Solanaceae" (Saporta, 1861).

The following year, 1862, Saporta started a series of papers in the *Annales des Sciences Naturelles* under the title *Études sur la végétation du sud-est de la France à l'époque Tertiaire*, "Studies on the vegetation of Southeast France in the Tertiary

period" systematically describing the fossils of Aix-en-Provence and the surrounding areas. In the second installment of this treatment (Ann. Sci. Nat. 4th series, vol. 17, page 262), Saporta formally described the fossil giving it the name of *Solanites brongniartii* and clearly referring the 1861 treaty. In that publication, he mentioned the existence of "at least" three specimens although only two were figured, with the second one cited as just "another corolla" (Figure 3.1). The third specimen was, at a later date (Saporta, 1873) recognized as the counterpart of the one upon which both descriptions were based.

In 1863, the first three installments were bounded and published together as the Volume 1 of a series of books bearing the same title. The fact that the description of *S. brongniartii* occupies page 109 in this compilation book has caused some confusion regarding the correct citation of the name. Therefore, in accordance to the ICBN (Vienna Code; McNeill et al., 2006), the correct name and citation for the genus should be *Solanites* Sap 1862 and type species *Solanites brongniartii* (Sap) Sap 1862 in Ann. Sci. Nat. Bot. ser. 4. 17: 262 with holotype MNHN-14215b.

Generic diagnosis— As given by Saporta (1862): *Corolla gamopetala, pentamera, rotata, æstivatione valvata, caduca. Stamina 5 corollæ fauci inserta, incumbentia, antheris 2-locularibus in processum apiculatum superne coalitis, longitudinaliter dehiscentibus*.

Generic description— Isolated flowers, presumably bisexual, actinomorphic. Calyx unknown. Corolla pentamerous, gamopetalous and caducous, with valvate aestivation, presumably rotate and reflexed. Androecium of five stamens alternate to

the corolla lobes with short filaments and elongated anthers. Anthers tapering distally and ending in a connective projection.

***Diagnosis of* S. brongniartii**— As given by Saporta (1862): *S. corolla quinquefida, lobis acuminatis, staminibus exsertis, incumbentibus, filamentis brevibus, antheris 2-locularibus fusiformibus, in processum tenuissime apiculatum desinentibus.*

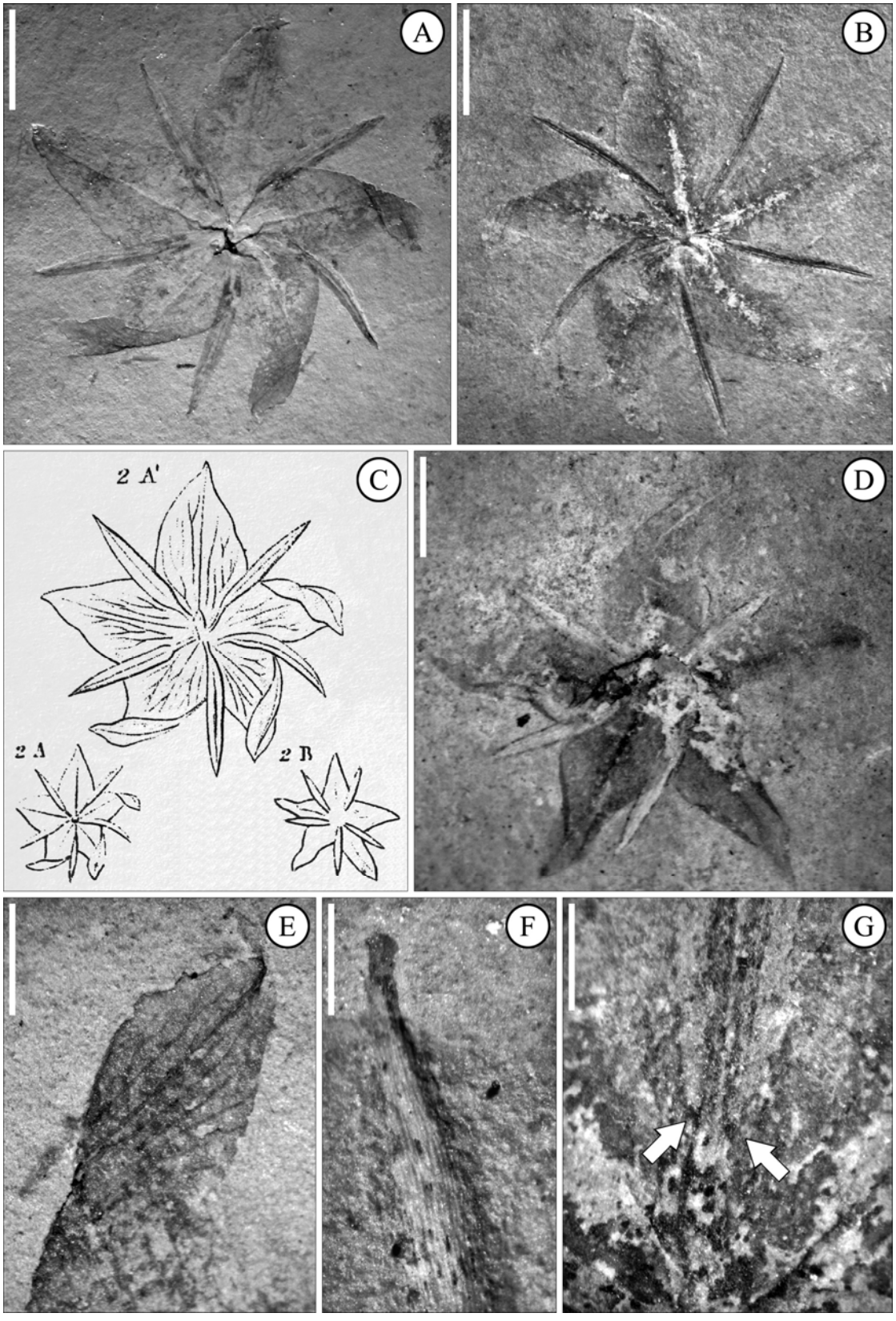
***Description of* S. brongniartii**— *S. brongniartii* is known from two isolated pentamerous flowers. One of the specimens represent a shed corolla (MNHN-14215a,b) while the second specimen appears to be a complete flower (MNHN-14223). The calyx is unknown. The corolla is membranaceous with basally fused and apically free petals, rotate, between 7.9 and 8.9 mm (mean 8.4 mm) in diameter. The free portion of the petals is between 1.7 and 2.4 mm wide (mean 2.0 mm) and between 3.0 and 3.5 mm long (mean 3.3 mm), the total length of the corolla is unknown. In the holotype, MNHN-14215b, the apices of three petals are folded over suggesting that in life the corolla was reflexed, probably tortuous (Figure 3.1.A-C). In the second specimen, MNHN-14223, the margins of the petals are broken and folded inward also suggesting a non-flat, reflexed corolla (Figure 3.1.D). Each petal has a conspicuous but not prominent midvein and several secondary veins parallel to the midvein that dichotomize towards the margin (Figure 3.1.E). The androecium is composed of five stamens that alternate with the petals. The filaments are short (Figure 3.1.G) and presumably epipetalous as they remained attached to the shed corolla (Figure 3.1.A-C). The anthers are between 3.0 and 3.7 mm long (mean 3.3 mm) and between 0.3 and 0.4 mm wide (mean 0.4 mm). The anthers have striated walls and end in a projection of the connective (Figure 3.1.F). One of the specimens (MNHN-14223) shows what

could be interpreted as the imprint of a two-carpelled gynoecium with separate styles and capitate stigmas (Figure 3.2). No fruits or vegetative structures had been associated with these flowers.

Locality— Laminated marly shales of the lower part, Aix-en-Provence Formation.

Age— When *S. brongniartii* was described, it was assigned a Late Eocene age by Saporta (1862, 1886). In the earlier part of the 20th century, the flora of Aix-en-Provence was cited as Sannoisien (i.e. Berry, 1916) and/or Aquitanien (i.e. specimen labels in MNHN), which corresponded to the Oligocene-Lower Miocene of North America (Osborn, 1907). Today, with the standardization of the Geological Time Scale, the name "Aquitanien" applies to the earliest stage of the Miocene and not to the Oligocene (Gradstein et al., 2004). New studies on the Aix-en-Provence Fm confirm that the age of the flora is Late Oligocene, Chattian (Châteauneuf and Nury, 1995; Kvacek and Erdei, 2001).

Figure 3.1. *Solanites brongniartii* (Sap) Sap. **A**. Type specimen (MNHN-14215b, formerly 14222), described by Saporta (1861, 1862) showing a pentamerous gamopetalous corolla and five stamens (bar = 2 mm). **B**. Counterpart of A (MNHN-14215a), described in Saporta (1873) (bar = 2 mm). **C**. Original drawings published by Saporta (1862), "2A" and "2A'" of specimen in A, "2B" of specimen in D. **D**. Second corolla (MNHN-14223) figured in Saporta (1862) showing pentamerous corolla and four of the five stamens (bar = 2 mm). **E**. Apex of one petal of MNHN-14215b (at 5:00 in A) showing membranaceous texture, folding of the tip and venation (bar = 1 mm). **F**. Apex of one stamen of MNHN-14215b (at 11:00 in A) showing apical connective projection (bar = 0.5 mm). **G**. Base of one stamen of MNHN-14215a showing attachment of anther (bar = 0.5 mm).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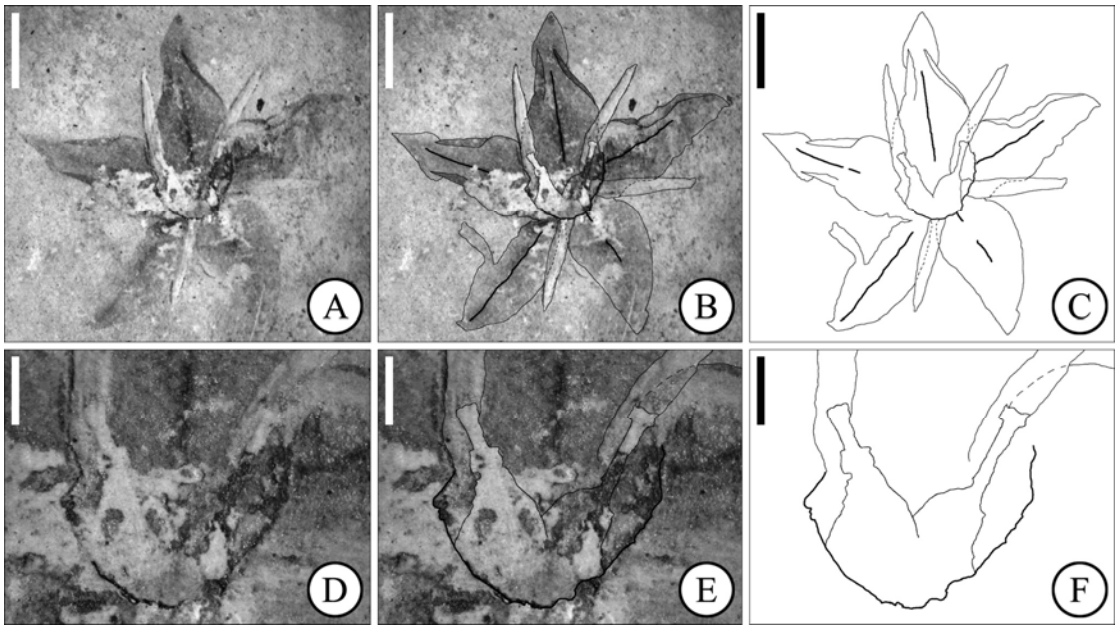

Figure 3.2. *Solanites brongniartii* (Sap) Sap (MNHN-14223). **A**. General view of flower (bar = 2 mm). **B**. General view of flower with traced outline (bar = 2mm). **C**. Outline of flower (bar = 2 mm). **D**. Close up of center of flower showing the imprint of two styles (bar = 1 mm). **E**. Center of flower with traced outline (bar = 1 mm). **F**. Outline of center of flower (bar = 1 mm).

In 1916, Berry described one specimen bearing two flowers as a second species of *Solanites* naming it *S. saportana*, a name that ought to be corrected to *S. saportanus* in order to agree in gender. The specimen was collected from the Holly Springs Sand, Claiborne Formation of Mississippi assigned at the time to the Wilcox Formation. In his original description Berry stated that "...the Wilcox flower described above … is very similar to *Solanites brongniarti*, although less completely preserved". Berry (1916) even reproduced some of the figures that Saporta used in his description of *S. brongniartii*, including those of the extant *Saracha* and *Wintheringia*. However, a closer look at the descriptions and the type specimens shows that the only resemblance between *S. saportanus* and *S. brongniartii* is their pentamery.

Three more species from the Claiborne Formation, were added by Berry in 1930; *S. sarrachaformis* –to be corrected to *S. sarachaformis* since the correct name for the extant genus is *Saracha* and not *Sarracha–*, *S. crassus* and *S. pusillus*. These three species are also based on pentamerous flowers with little else in common.

***Description of* S. saportanus**— The type specimen of this taxon shows two flowers, one in side view and one in bottom view suggesting that the two flowers were close together in life, possibly on the same inflorescence axis (Figure 3.3.A-C). The flowers are small (5.8 mm diameter) with a shallow floral cup. The calyx is thick, pentamerous gamosepalous with small rounded to slightly acuminate calyx lobes that show traces of a midvein. The calyx is 2.6mm in diameter, with each calyx lobe (sepal) measuring between 1.2 and 1.5 mm wide (mean 1.3 mm) and between 0.5 and 0.8 mm (mean 0.65 mm) long. The corolla is also pentamerous with small, coriaceous, concave, acuminate petals whose free portion measures between 1.6 and 2.2 mm

(mean 1.42 mm) wide and between 2.3 and 2.7 mm (mean 2.5 mm) long. It is unclear if the petals were completely free, born on the rim of a hypanthium (implying adnation of calyx and corolla), or if they were fused at the base and free at the tips, where the separation would occur at a level obscured by the calyx. The corolla seems to have been opposite to the calyx, with each petal directly in front of a sepal. Berry (1916) reported the existence of stamens in this specimen, however, it was not possible to find evidence of them. There are no traces of gynoecium. A second specimen (Table 3.6) does not show additional characters. The holotype of this species is USNM-35990.

Table 3.6. Specimens identified as *S. saportanus*.

Housing Institution	Collector	Locality	Formation	State	Specimen #
USNM	Berry	Holly Springs	Claiborne	MS	35990
FMNH	Dilcher et al.	Bovay Clay Pit	Claiborne	MS	UF8222 / UF8222’

***Description of* S. pusillus**— This taxon was described from three specimens, three syntypes (Table 3.7). One of them represent a flower in face (top) view (Figure 3.3.D-F), one is a flower in bottom view (Figure 3.3.G-I) and the third one is a flower in side view (Figure 3.3.J-L). These flowers are small, from 7.2 to 9.9 mm in diameter (mean 8.7 mm), and have always been found isolated. The flowers are pentamerous, with a shallow, thick, well developed hypanthium, semicircular (U-shape) to cupulate in shape (Figure 3.4.A). On top view, the rim of the floral cup is very thick, ring-shaped (Figure 3.3.D-F, 3.4.D-F), sometimes slightly lobed and interpreted as a nectary ring that measures between 1.6 and 4.2 mm in diameter (mean 3.4 mm). The five parts that form the perianth cannot be defined as sepals or petals in the type specimens (Figure 3.3.D-L), but additional specimens (Table 3.7) with both whorls

preserved indicate that they represent sepals (Figure 3.4.C-F). These sepals are triangular in shape, between 1.5 and 2.8 mm wide (mean 2.14 mm), and between 1.5 mm and 3.5 mm long (mean 2.6 mm), with a prominent midvein or keel sometimes with additional smaller ridges at either side (Figure 3.3.D-F, J-L). In addition, they are covered by abundant filiform hairs (Figure 3.4.B). The petals alternate with the sepals (Figure 3.4.C-F), they are membranaceous with some faint veins, small, cucullate ("hooded") and possibly clawed, between 3.2 and 3.4 mm in length (mean 3.3 mm) and 0.9 and 1.5 mm (mean 1.1 mm) in width. There are five stamens, opposite the petals (Figure 3.4.E, F), each stamen is about 3.4 mm in length with a 0.4 mm long tetrasporangiate anther. The pollen grains appear to be tricolporate (Figure 3.5.A, B) with striate-rugulate exine (Figure 3.5.C, D), they are between 16 and 21 μm in length. In most specimens, the gynoecium is not discernible but in the type specimen in side view, it appears to be superior with one relatively thick style and one stigma (Figure 3.3.J-L) which would make the flower, perigynous. This species has three syntypes housed at the Smithsonian Institution with numbers USNM-222831, USNM-222832, and USNM-39950.

Table 3.7. Specimens identified as *S. pusillus*.

Housing Institution	Collector	Locality	Formation	State	Specimen #
USNM	Berry	Holly Springs or La Grable[a]	Claiborne	TN	222831
USNM	Berry		Claiborne	TN	222832
USNM	Berry		Claiborne	TN	39950
FMNH	Dilcher et al.	Bolden Pit	Claiborne	MS	UF8214 / UF8214'
FMNH	Dilcher et al.	Bovay Clay Pit	Claiborne	MS	UF8223 / UF8223'
FMNH	Dilcher et al.	Bovay Clay Pit	Claiborne	MS	UF8226
FMNH	Dilcher et al.	Bovay Clay Pit	Claiborne	MS	UF49566 / UF49566'
FMNH	Dilcher et al.	Bovay Clay Pit	Claiborne	MS	UF49568 / UF49568'
FMNH	Dilcher et al.	Warman Clay Pit	Claiborne	TN	UF33557 / UF33557'
UCPC	Crepet	Warman Clay Pit	Claiborne	TN	UCPC (5)
UCPC	Crepet	Puryear	Claiborne	TN	UCPC "P5" (18)
UCPC	Crepet	Puryear	Claiborne	TN	UCPC "P" (3)
UCPC	Crepet	Puryear	Claiborne	TN	UCPC "P10" (22)
UCPC	Crepet	Puryear	Claiborne	TN	UCPC "P" (13)
IUPC	Crepet	Miller	Claiborne	TN	IUPC M2203[b]

[a]-Berry (1930) did not identify the locality for each specimen, but noted that only one specimen came from La Grable. [b]-this specimen was examined on photographs archived in the paleobotanical laboratory collection.

Figure 3.3. Type specimens of North American *Solanites*. **A-C**. *S. saportanus* Berry 1916 (USNM-35990; bar=2 mm) showing two flowers. **A**. General view of flowers. **B**. General view of flowers with traced outlines. **C**. Outline of flowers. **D-L**. *S. pusillus* Berry 1930. **D-F**. USNM-222831 (bar=2 mm). **D**. General view of flower showing five "petals" and thick throat. **E**. General view of flower with traced outline. **F**. Outline of flower. **G-I**. USNM-222832 (bar=2 mm). **G**. General view of flower. **H**. General view of flower with traced outline. **I**. Outline of flower. **J-L**. USNM-39950 (bar=2 mm). **J**. General view of flower showing part of the pedicel. **K**. General view of flower with traced outline. **L**. Outline of flower.

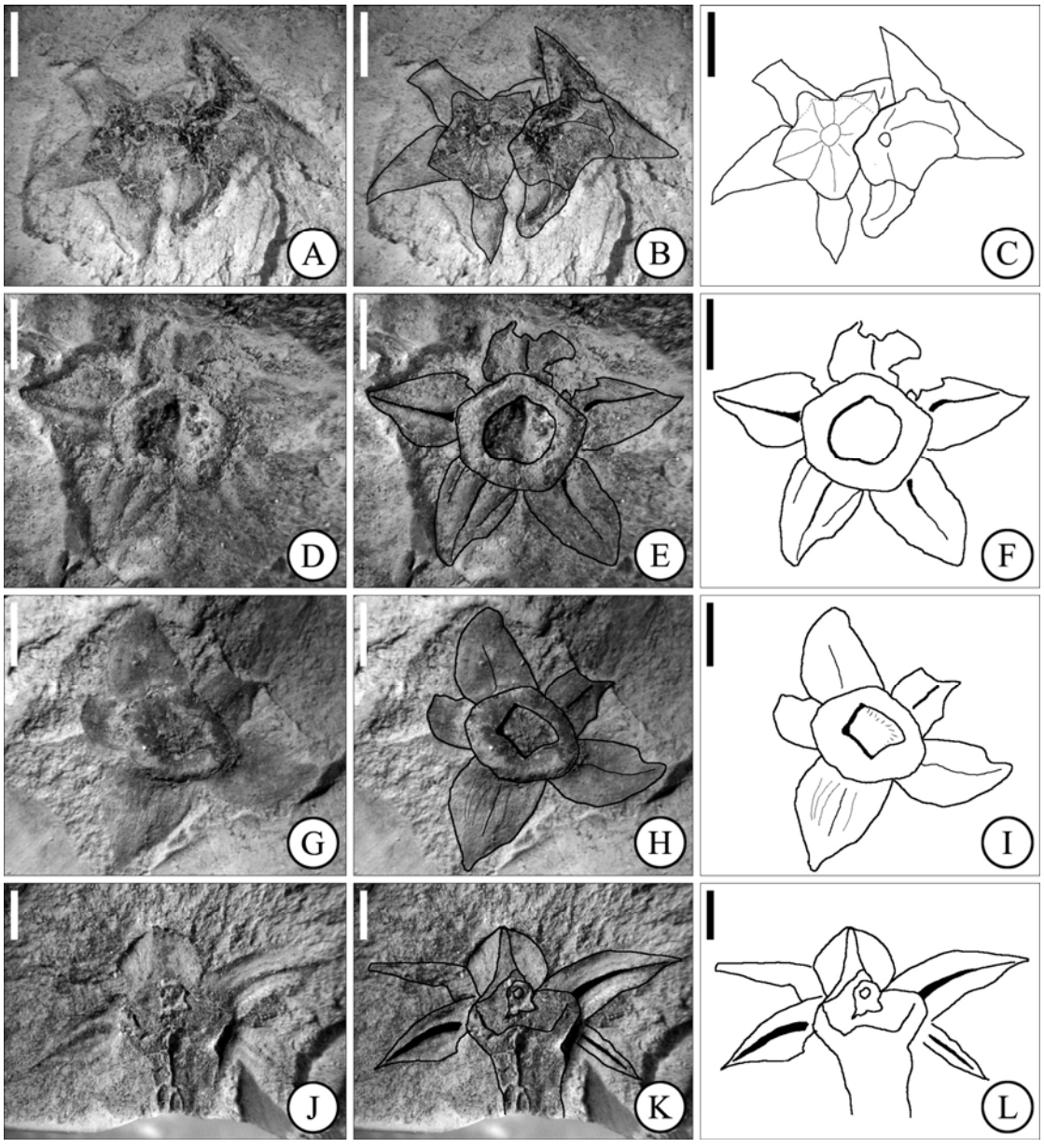
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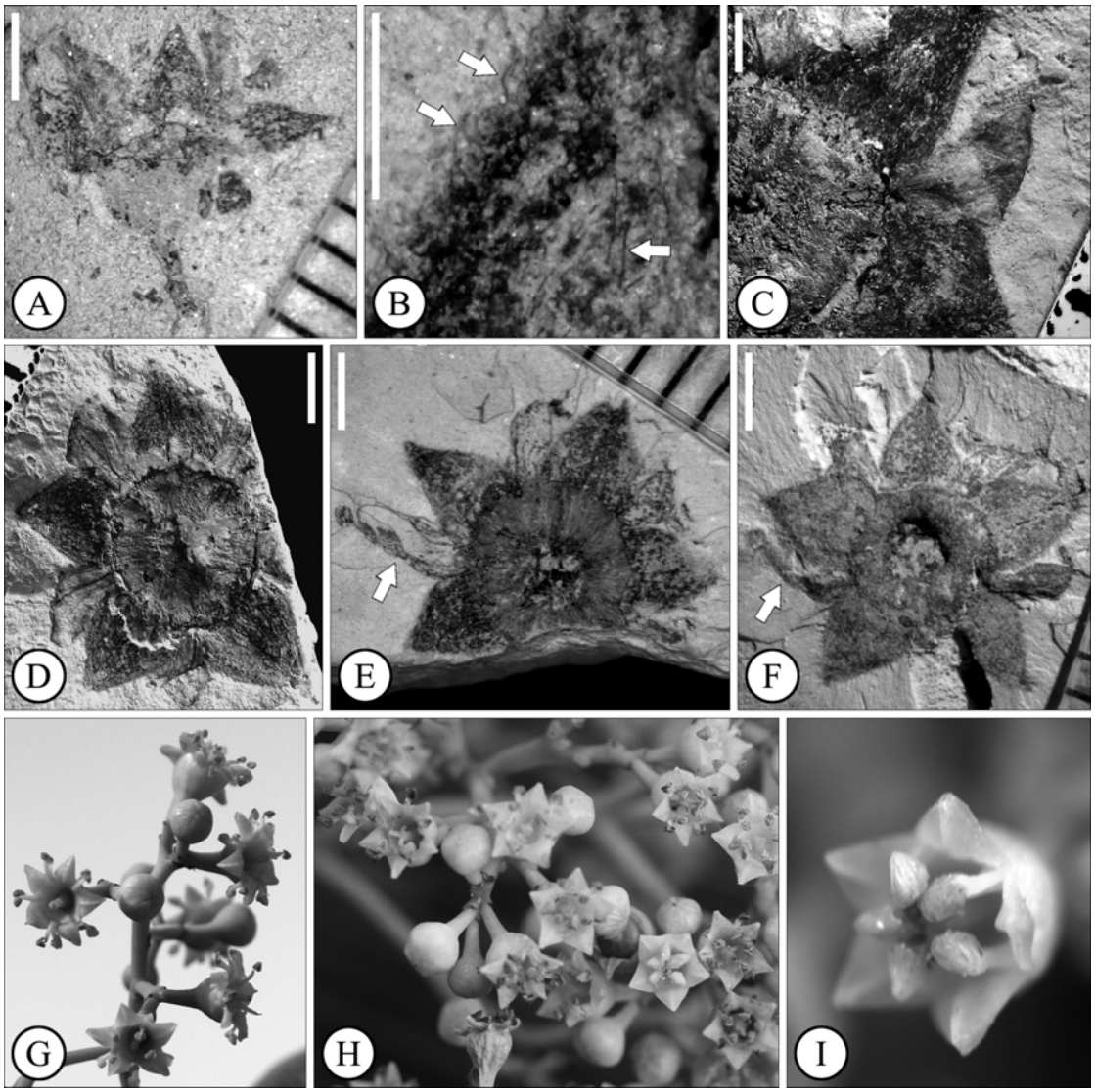
Figure 3.4. *Solanites pusillus* and extant *Ziziphus* (Rhamnaceae). **A**. Flower in lateral view showing circular floral cup (UF-8226; bar=2 mm). **B**. Close up of sepal showing abundant filiform trichomes (UF-46566; bar=0.5 mm). **C**. Cucullate petal showing membranaceous texture (UF-49568; bar=1 mm). **D**. Bottom view of flower showing sepals and membranaceous petals with conspicuous venation (UF-49568'; bar=2 mm). **E**. Top view of flower showing sepals with midvein, cucullate petals, stamen opposite to petal (arrow) and thick nectary disk rim (UF-49566'; bar=2 mm). **F**. Top view of flower showing thick nectary ring, sepals, cucullate petals and stamen enclosed by petal at arrow (UF-49566; bar=2 mm). **G**. Extant *Ziziphus sp* (Rhamnaceae) showing circular floral cup similar to the one shown in A. **H**. Extant *Ziziphus rignonii* showing flowers in top view with five sepals with keels and five petals enclosing opposite stamens. **I**. Flower of extant *Ziziphus rignonii* showing prominent keels in each sepal and the five petals enclosing five stamens.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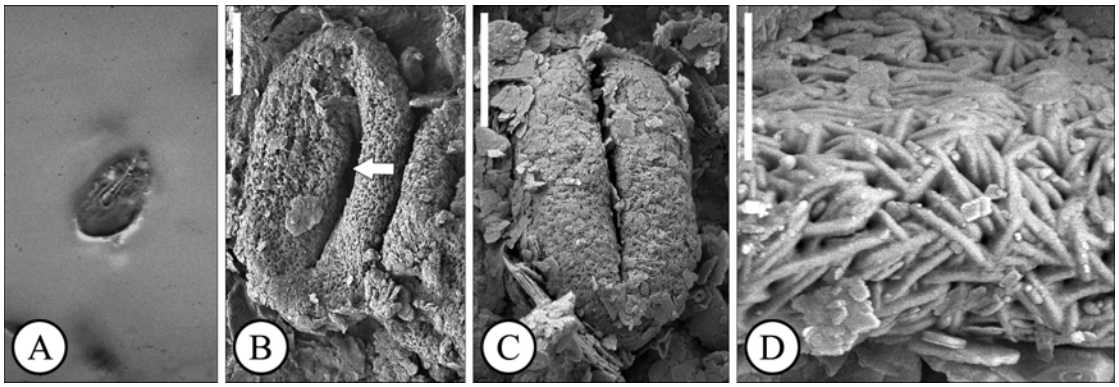


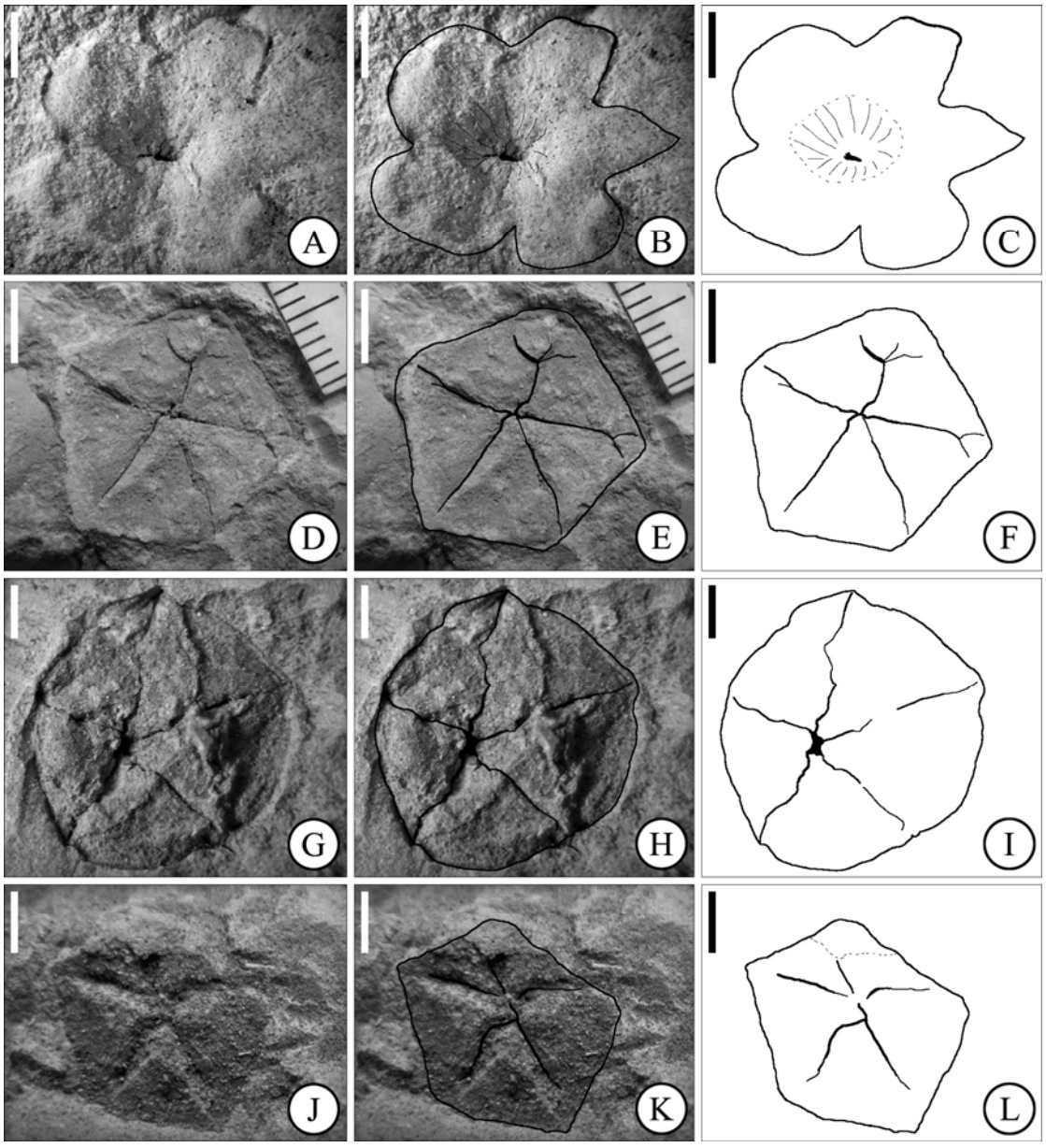
Figure 3.5. Pollen grains of *Solanites pusillus*. **A**. Micrograph of pollen grain showing a pore and part of a colpus (IUPC-M2203). **B**. SEM picture of CUPC-1732 (UF-49566) showing one pollen grain with colpus and foldings suggesting a pore (arrow) (bar=6 μm). **C**. SEM picture of CUPC-1727 (UCPC-P10) showing one pollen grain with exine ornamentation and a colpus (bar=6 μm). **D**. Detail of exine ornamentation in C (bar=1.2 μm).

***Description of* S. sarachaformis**— The type specimen of this taxon is an impression of a flower with no organic matter left (Figure 3.6.A-C). The flower measures about 1 cm in diameter. It is pentamerous with a shallow floral cup (Figure 3.6.A-C). The units that form the perianth are fused towards the base and free towards the tips, they are some 3 mm in width and some 2.6 mm long. It is not clear if they represent calyx lobes or corolla lobes. There are no traces of stamens or gynoecium. Additional specimens comparable to this fossil are also in bad preservational state (Table 3.8). The type for this species is USNM-35948.

Table 3.8. Specimens identified as *S. sarachaformis*.

Housing Institution	Collector	Locality	Formation	State	Specimen #
USNM	Berry	Holly Springs	Claiborne	TN	35948
FMNH	Dilcher et al.	Bovay Clay Pit	Claiborne	MS	UF49569 / UF49569’

Figure 3.6. Type specimens of North American *Solanites*. **A-C**. *S. sarachaformis* Berry 1930 (USNM-35948; bar=2 mm). **A**. General view of flower. **B**. General view of flower with traced outlines. **C**. Outline of flower. **D-L**. *S. crassus* Berry 1930. **D-F**. USNM-39949a (bar=5 mm). **D**. General view of gamopetalous corolla. **E**. General view of corolla with traced outline. **F**. Outline of corolla. **G-I**. USNM-39949b (bar=2 mm). **G**. General view of corolla. **H**. General view of corolla with traced outline. **I**. Outline of corolla. **J-L**. USNM-39949c (bar=2 mm). **J**. General view of pentamerous corolla. **K**. General view of corolla with traced outline. **L**. Outline of corolla.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***Description of* S. crassus**— This taxon is represented only by three syntypes and the three are poorly preserved (Table 3.9). Although there is still some original matter left, there is almost no structural detail. The impressions seem to be of a membranaceous corolla where the petals are fused throughout their length. They are between 8.1 and 16.5 mm (mean 11.7 mm) in diameter. Two of the specimens are pentagonal in outline (Figure 3.6.D-F, J-L) while the third is circular (Figure 3.6.G-I).

Table 3.9. Specimens identified as *S. crassus*.

Housing Institution	Collector	Locality	Formation	State	Specimen #
USNM	Berry	Holly Springs	Claiborne	TN	39949a
USNM	Berry	Holly Springs	Claiborne	TN	39949b
USNM	Berry	Holly Springs	Claiborne	TN	39949c

Age— The fossils assigned the different *Solanites* species were originally assigned to the Lower Eocene Wilcox Formation (Berry, 1916, 1930). However, after thorough palynological studies, these sediments are assigned today to the Middle Eocene Claiborne Formation (Dilcher, 1971; Potter, 1976).

CANTISOLANUM DATUROIDES

This fossil was described by Reid et Chandler (1933) from the London clay. It is known only from one specimen, NHM-V.23096 housed at the Natural History Museum in London, UK. The specimen was dissected by Reid and Chandler and today consists of one seed and part of a capsule. The seed is ovoid in shape (Figure 3.7), 4.5 mm long by 3.6 mm wide and 1.8 mm thick. There seems to be a micropylar region and a funicular region obliquely positioned with respect to it. There also seems to have had ridges radiating from the micropylar region, although the nature of these

ridges is not immediately obvious. The specimen has few structural details and more have been obscured by pyrite oxidation.

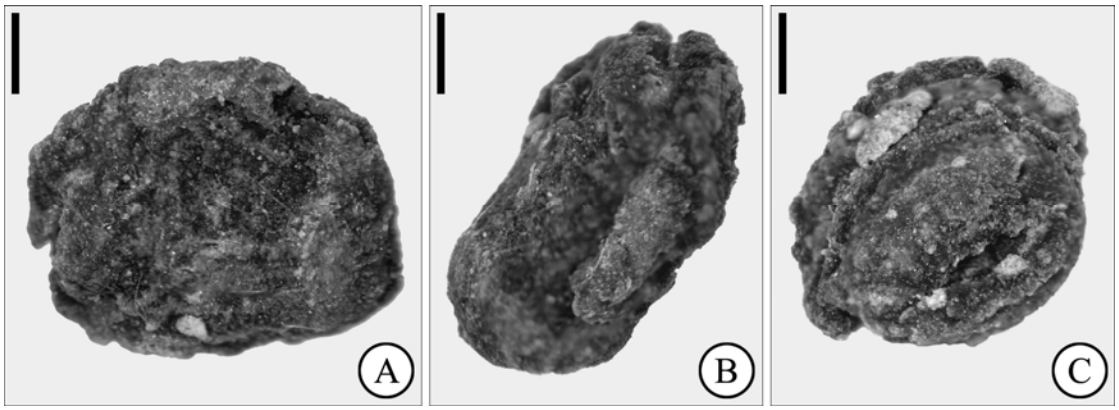

Figure 3.7. Type specimen of *Cantisolanum daturoides*. **A**. Lateral view of seed (bar=1 mm). **B**. Top view of seed (bar=1 mm). **C**. Front view of seed (bar=1 mm).

CLADISTIC ANALYSIS

***Analysis with* S. brongniartii**— The phylogenetic analysis of the Bremer et al. (2002) molecular matrix yielded two trees. Although they show the same general backbone as the Bremer et al. (2002) strict consensus of 24 trees, there are some differences (not shown). The first is in the relationship of the outgroups, in our analysis *Vitis* and *Dipentodon* are not sister groups, instead *Vitis* is sister to the Asteridae. Within the Asteridae, the four clades, Cornales, Ericales, Lamiids and Campanulids are each monophyletic and have the same relationships as in the Bremer et al. (2002) consensus tree: (Cornales(Ericales(Lamiids, Campanulids))). Within Ericales and Campanulids, the basal polytomies shown in Bremer et al. (2002) are resolved in our analysis. And in the Lamiids, some relationships among major clades have changed, for example, in our analysis, the Icacinaceae resolves as monophyletic

with *Oncotheca* moving to a position as sister to the Garryales instead of a clade *Oncotheca-Apodytes* and a second clade of the rest of the Icacinaceae as in Bremer et al. (2002). Another major difference is the relationship of the Lamiid clades that in Bremer et al. (2002) is (Gentianales (Vahliaceae Boraginaceae)(Lamiales Solanales including Convolvulaceae)) but in our analysis is ((Convolvulaceae Boraginaceae) Lamiales)(Vahliaceae (Solanales Gentianales)). Except for the position of Convolvulaceae, the differences pertain to families unplaced to order and to the relationships among orders, not to membership to those orders.

The analysis of the total evidence matrix resulted in 83 most parsimonious trees (MPTs). The strict consensus of these trees (Figure 3.8) shows that the fossil taxon, *Solanites brongniartii*, is found in a polytomy in the first node of the Euasteridae along with eight individual terminals and nine clades. This placement is supported by a 90% bootstrap value but it is also suggestive of the "floating" nature of the fossil taxon. In the strict consensus a change in character 14, attachment of the stamens, from attachment to the receptacle (free stamens) to attachment to the petals (epipetaly) supports this group; however, optimization in each of the MPTs does not result in this change at this node and in fact, no morphological character defines this group.

A closer look to the 83 MPTs reveal that *Solanites brongniartii* floated between only six different positions (Figure 3.9). These are: (1)as sister to *Vahlia* in 13 trees (Figure 3.9.A) supported by a change from a widening to an open corolla (ch. 4) and a change from one to two styles (ch. 22), (2)as sister to *Oncotheca* in 8 trees (Figure 3.9.B) supported by a short filament (ch. 15) and the presence of a connective projection (ch 17), (3)in a polytomy with *Oncotheca* and *Apodytes* in 5 trees (Figure

3.9.C) supported by the same characters as in the previous position as *Apodytes* is not present in the morphological matrix, (4)nested within Aquifoliales as sister to a clade made of *Helwingia* and *Phyllonoma* in 19 trees (Figure 3.9.D), this position is supported by the membranaceous texture of the corolla (ch. 8) shared with *Phyllonoma* (ambiguous for *Helwingia*) and the petal midvein (ch. 10) shared with *Helwingia* (ambiguous for *Phyllonoma*), (5)nested within Solanales as sister to the Montiniaceae (Figure 3.9.E) in 19 trees supported by a change from widening to open corolla (ch. 4), and (6)as sister to *Olea* in 19 trees (Figure 3.9.F) supported by a short filament (ch. 15) and a projection of the connective (ch. 17).

The analysis “without gynoecium characters” resulted in 27 MPTs (not shown). These trees are a subset of the 83 trees found when *S. brongniartii* is interpreted as having a bicarpellate gynoecium with separate styles and capitate stigmas. In these trees, *S. brongniartii* floated between two positions: as sister to *Olea* in 19 trees and as sister to *Oncotheca* in 8 trees. In both cases, the relationships is supported by a short filament (ch. 15) and the presence of a connective projection (ch 17).

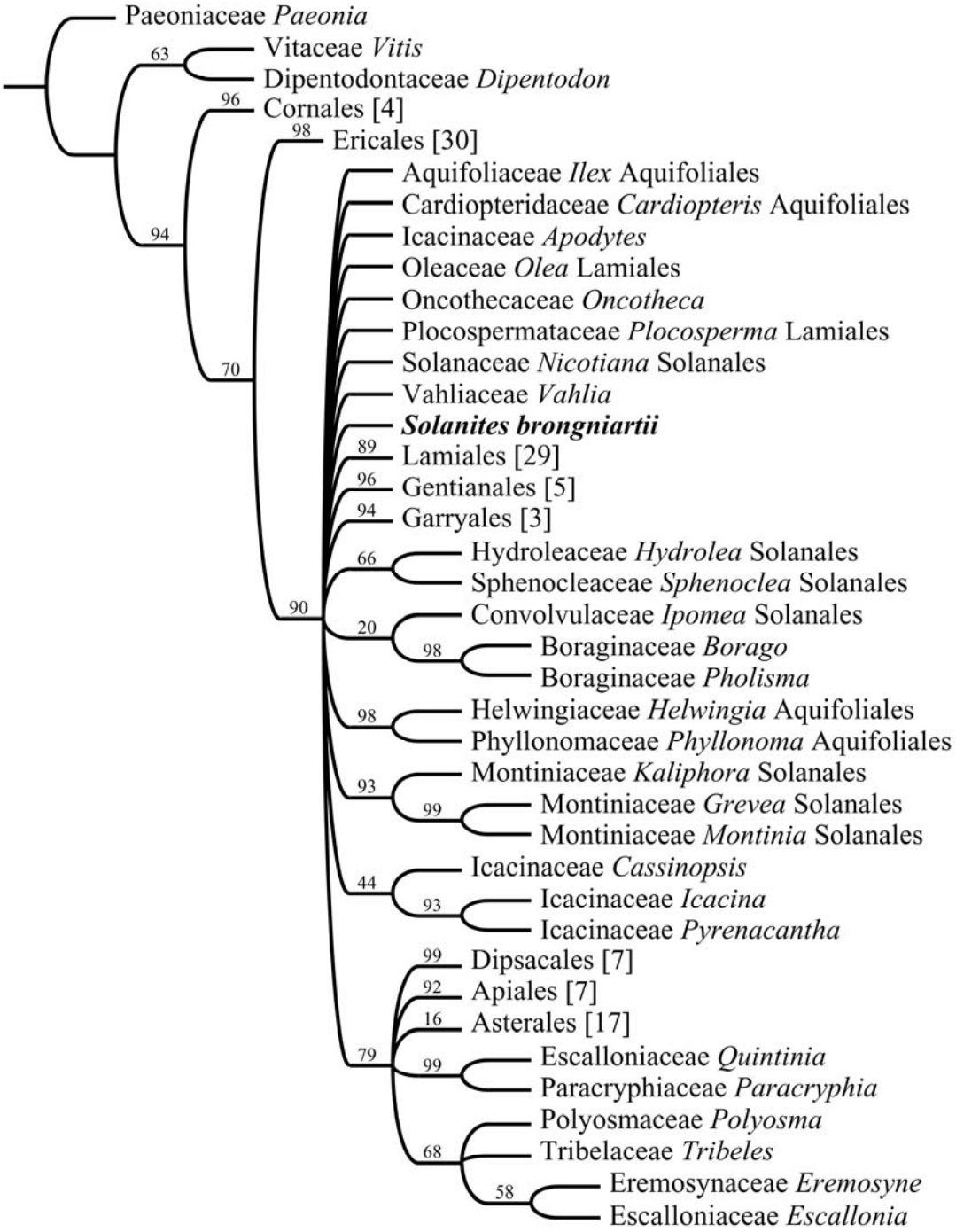

Figure 3.8. Strict consensus of 83 trees (L=56326, CI=32, RI=48). Numbers in square brackets indicate taxa in that collapsed branch. Bootstrap values above branches.

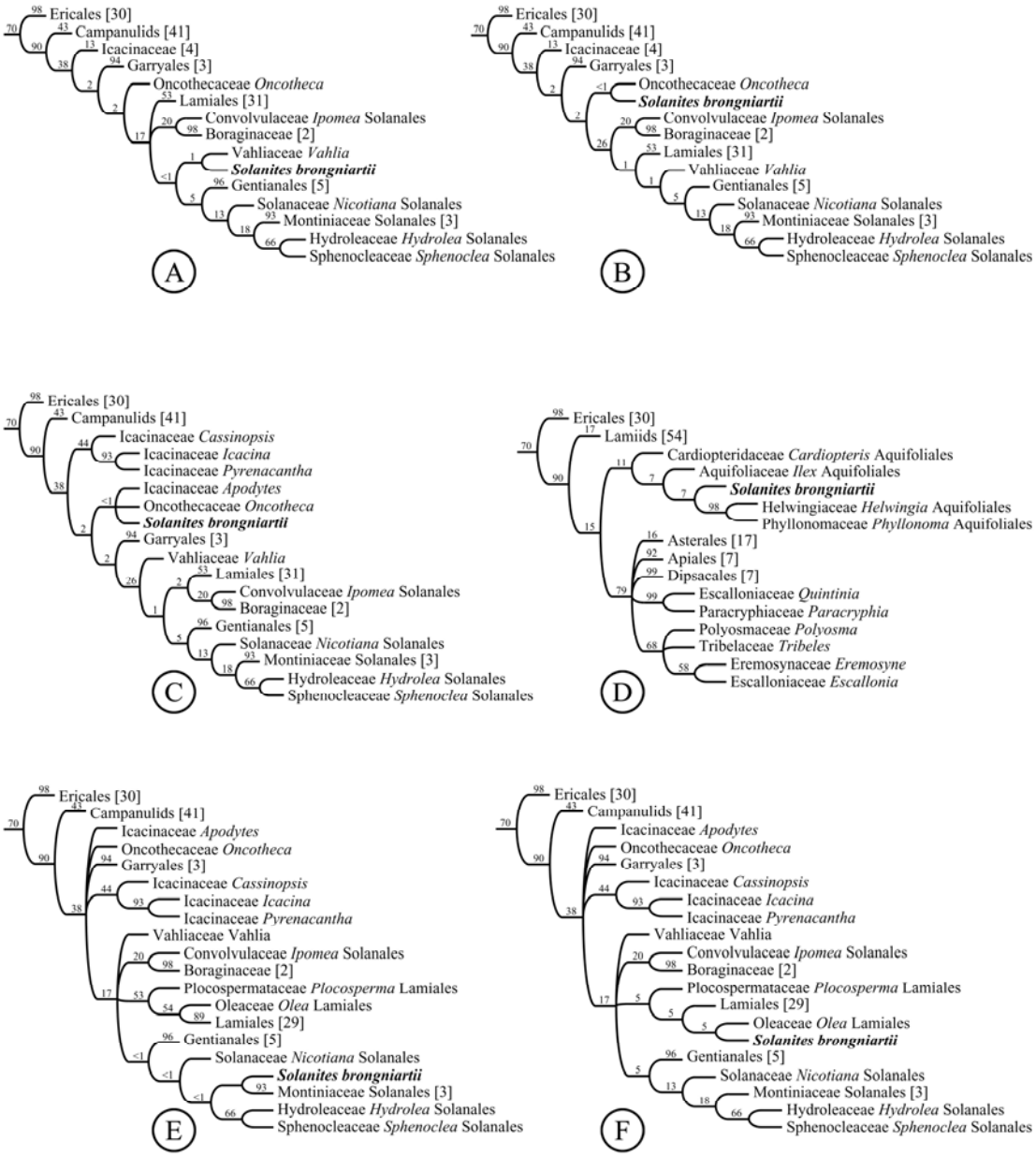

Figure 3.9. The six alternative positions that *Solanites brongniartii* occupies in the 83 MPT. **A**. As sister to *Vahlia* (13 trees). **B**. As sister to *Oncotheca* (8 trees). **C**. In a polytomy with *Oncotheca* and *Apodytes* (5 trees). **D**. Nested within the Aquifoliales (19 trees). **E**. Nested within the Solanales (19 trees). **F**. As sister to *Olea* (19 trees)

The analysis of the combined matrix without the fossil resulted in 19 MPTs (L=56322, CI=32, RI=48). As expected, the strict consensus (not shown) is more resolved than in the analysis including the fossil. However, polytomies abound. For example, the Asterales / Apiales / Dipsacales / *Quintinia-Paracryphia* / *Polyosma-Tribeles-Eremosyne-Escallonia* polytomy (Figure 3.8) is present in the consensus with or without the effect of the fossil. The same occurs with *Apodytes*, *Oncotheca*, Icacinaceae (remaining 3 taxa) and Garryales, their relationships remain uncertain when the fossil is excluded. When the fossil is not included, the higher-nested lamiid groups form a monophyletic group with a basal polytomy of the structure: *Vahlia* / Lamiales (31 taxa) / Solanales-Gentianales / Convolvulaceae-Boraginaceae. With the fossil, this monophyletic group collapses and so does the Solanales, but the Lamiales only lose the first two diverging taxa, the remaining 29 still form a clade. In summary, the addition of the fossil resulted in only about 5 significant node collapses in the strict consensus.

The "character by character" analysis revealed that turning off ten of the characters had no impact on the results as the MPTs obtained were the same obtained when all characters are included (Table 3.10). In most of the other cases, removal of one character resulted in a subset of the 83 MPTs obtained when all characters were included. The only two characters whose removal resulted in new trees are corolla fusion (ch. 7) and stamen attachment (ch.14). The analysis with stamen attachment removed (ch. 14) is also the only in which a larger set of trees was found (Table 3.10).

Table 3.10. Number of MPTs and position of the fossil taxon, *Solanites brongniartii*, when each morphological character was excluded from the analysis. *-indicates analyses that produced different topologies from the 83 obtained when all characters were included. -- indicates analysis not performed (uninformative character).

Character excluded	MPT	Position(s) of *Solanites brongniartii*
1 Flower sexuality	83	same
2 Flower size	83	same
3 Corolla symmetry	83	same
4 Corolla shape	8	sister to *Oncotheca*
5 Corolla aestivation	12	sister to *Olea* or to Montiniaceae (Solanales)
6 Corolla merosity	83	same
7 Corolla fusion	14*	various positions within Solanales, sister to *Olea*, *Ilex*, *Vahlia*, or a *Vahlia*-Solanales-Gentianales clade
8 Corolla texture	5	in a polytomy with *Apodytes* and *Oncotheca*
9 Corolla persistence	19	sister to *Helwingia-Phyllonoma* (Aquifoliales)
10 Petal midvein	5	in a polytomy with *Apodytes* and *Oncotheca*
11 Apices of petals	83	same
12 Stamen number relative to petals	83	same
13 Stamen cycle orientation	83	same
14 Stamen attachment	97*	same 6 positions plus as sister to a *Vahlia*-Solanales-Gentianales clade, in a polytomy with *Nicotiana* and other Solanales, or in a polytomy with *Hydrolea* and *Sphenoclea*
15 Filament vs. anther	32	sister to *Ilex* or to *Vahlia*
16 Anther surface	--	--
17 Connective projection	51	sister to *Ilex*, *Vahlia* or Montiniaceae (Solan.)
18 Anther dehiscence	83	same
19 Stamen vs. corolla lobes	83	same
20 Carpel number	83	same
21 Ovary	--	--
22 Number of styles	51	sister to *Oncotheca*, *Olea*, or Montiniaceae
23 Stigma shape	6	sister to *Olea*

***Analysis with* S. pusillus**— The phylogenetic analysis of the combined matrix resulted in two trees whose only difference is the position of the fossil taxon *Solanites pusillus* as either sister to *Condalia* or to *Krugiodendon* (Figure 3.10). The backbone of the cladogram is more similar to the *rbcL* cladogram of Richardson et al. (2000) than to their *trnL* or combined *rbcL* / *trnL* tree. In the analysis the Rhamnaceae is resolved as monophyletic with a bootstrap value of 87, although within the Rhamnaceae the support for the different clades is generally low. The two fossils described by Calvillo-Canadell and Cevallos-Ferriz (2007), *Nahinda axamilpensis* and *Coahuilanthus belindae* are found well nested in different clades, as sisters to *Colubrina* and *Sageretia* respectively.

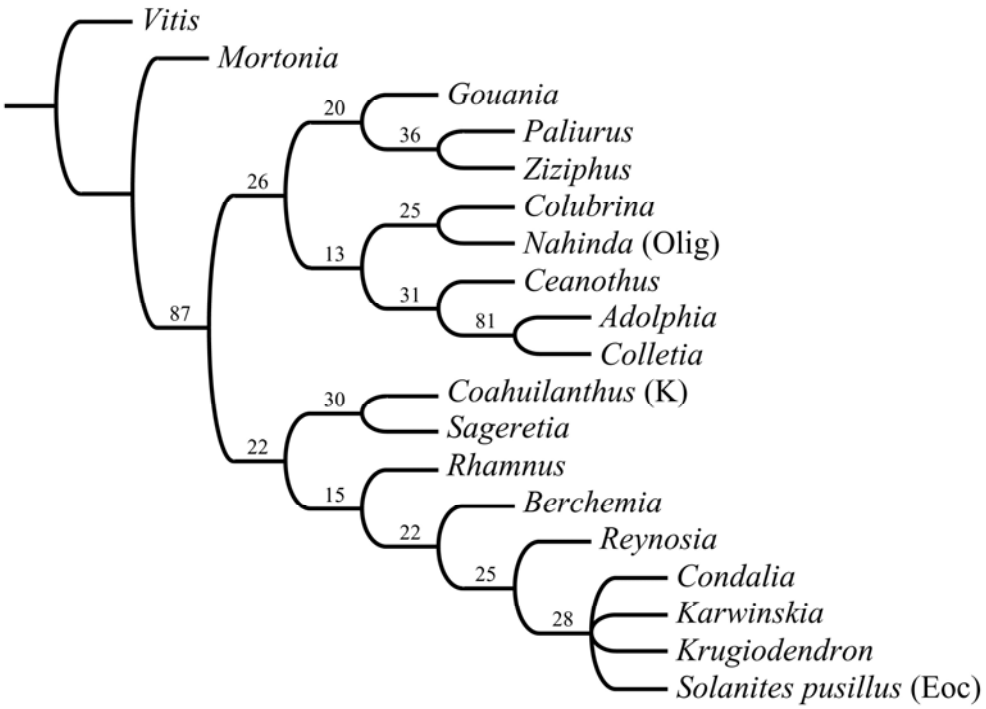

Figure 3.10. Strict consensus of 2 trees (L=1024, CI=75, RI=70). Bootstrap values above branches. K-Cretaceous, Eoc-Eocene, Olig-Oligocene.

DISCUSSION

The study of the type specimens of the fossil species once assigned to Solanaceae has shed important light into the identities of these fossils. One of the most important conclusions is that the five fossil species of the genus *Solanites* do not belong to the same or even related taxa. For example, *S. pusillus* and *S. saportana* do not have a gamopetalous corolla, one of the diagnostic characters of the genus (Figure 3.3). The corolla is gamopetalous in *S. crassus*, but it is not rotate and it does not have corolla lobes (Figure 3.6.D-L). In *S. sarachaformis*, it is not clear if the impression represents a calyx or a floral cup, but it is not rotate (Figure 3.6.A). In the case of the stamens, they have short filaments and long fusiform anthers in the type (Figure 3.1) while in *S. pusillus*, the only other species with known anthers, they have long filaments and globose anthers (Figure 3.4.E, F). Not only does each of the North American species differ significantly from the type species, they also differ amongst each other indicating that none of the five species belong in the same genus. In fact, the only character shared by the five species is their pentamery.

***Affinities of* S. brongniartii**— In gross morphology, *S. brongniartii* does show some solanaceous characters such as the pentamerous rotate corolla with reflexed corolla lobes (petals) and the stamens with long anthers and short filaments. (Figure 3.1). These characters are typical of the genus *Solanum* itself and they are so conspicuous in the fossil that it was originally assigned to the genus *Solanum* (Saporta, 1861). However a closer look reveals that there are structural differences which result in the fossil not fitting completely into the genus. For example, the anthers in the genus *Solanum* typically have poricidal dehiscence, in the fossil there is no evidence of such pores, instead, the apices of the anthers end in a connective projection. Longitudinal dehiscence is found elsewhere in the Solanaceae, including

some species of *Solanum* (Carrizo García et al., 2008), but in these instances the anthers lack a connective projection.

Another character that is present in *S. brongniartii* but is not found in the Solanaceae is the gynoecium with two styles and two stigmas. In the Solanaceae, the ovary is typically composed of two completely fused carpels, with one style and one stigma. This character calls into question the assignment of *S. brongniartii* to the Solanaceae. Interestingly, when the gynoecium is coded as "unknown" (the character states for three gynoecium characters are changed to "?"), *S. brongniartii* is not placed close to the Solanaceae either.

A family where divided styles, tortuous corolla and capitate stigmas occur, all present in *S. brongniartii*, is the Apocynaceae. However, the fossil does not show the specialization seen in that family (appendages, outgrowths, etc) especially in the stamens. The same could be said about the Boraginaceae, another family that the fossil superficially resembles.

The phylogenetic analysis in which *S. brongniartii* was included, did not place the fossil in a defined position (Figure 3.8). Instead it produced six different placements (Figure 3.9). Interestingly, none of them related to the Apocynaceae or to the Boraginaceae. However one of the alternatives relates to the Solanales, not as sister to the Solanaceae but as sister to the Montiniaceae (Figure 3.9.E). This result highlights the mosaic nature of this fossil taxon that combines characters that today are found in different taxa.

One conclusion that can be drawn from the phylogenetic analysis is that *S. brongniartii* is a member of the Euasteridae (Figure 3.8). Five of the six alternatives place the fossil taxon in the Lamiid clade while only one places it in the Campanulid clade, within the Aquifoliales (Figure 3.9). A closer look to the characters that support the different placements reveal that they tend to be the same, for example, a change from a widening corolla (campanulate, infundibiliform) to an open corolla (ch. 4) supports the *Solanites*-Montininaceae clade as well as the *Solanites*-*Vahlia* clade. The same occurs with the short filament (ch 15) and the connective projection (ch. 17); they support the clade *Solanites*-*Oncotheca* as well as the clade *Solanites*-*Olea*. This suggests that these characters are highly homoplasic and that the rest of the characters do not contribute significantly to the establishment of the relationships of *Solanites brongniartii*.

This idea is confirmed for at least ten characters as their removal did not change the number of trees obtained in the analysis or the positions of *Solanites* in those trees (Table 3.10). For nine other characters, removal resulted in a subset of the original trees (Table 3.10), suggesting once again that *Solanites* has a combination of characters that is not found in extant taxa. For this reasons, it is suggested that *S. brongniartii* be accepted as a bona fide euasterid. Many characters of *S. brongniartii* are still unknown; discovery of those character states can shed more light into its relationships but until more specimens are discovered, and more refined phylogenetic analyses are performed –for example by breaking down highly polymorphic taxa into more discreet units– the best placement for the fossil is as *insertae sedis* within the Euasteridae.

***The North American* Solanites**— As discussed earlier, the four *Solanites* species from North America show little resemblance to the type species of *Solanites* and should therefore, be removed from the genus and possibly from the family as well. *S. crassus* is the only one of the four species that show a solanaceous morphology, the presumably membranaceous infundibuliform corolla. But this character, although not widespread among flowering plants, is not exclusive of Solanaceae; its sister family, the Convolvulaceae also shows this morphology. The lack of other structural characters prevents a more definite identification at this time, but it seems plausible that these fossils represent a member of the Solanales. They do not, however, represent a member of the genus *Solanites*.

S. sarachaformis is another species with few characters as only the outline of the flower is preserved, with no structural detail. From the fossil it is not possible to distinguish if the imprint is of a calyx or a floral cup. But, judging from the shape and depth of the imprint in the sediment, it seems these perianth parts were somewhat fleshy, as a thin, delicate tissue would have left a flatter imprint. It is possible that *S. sarachaformis* represents the external mold of other taxa that, when with organic material, is identified as a different species. The imprint, however, could not have been made by a *S. brongniartii*-looking flower because the size and shape of the lobes is not consistent with the dimensions of *S. brongniartii*.

The remaining two species, *S. saportanus* and *S. pusillus*, show more structural detail than the previous ones, allowing for a more critical comparison. In gross morphology and general view the two species seem very similar, but a closer look reveals important differences. Both species have a shallow, thick, cupulate floral cup, but that of *S. pusillus* clearly shows the insertion of the sepals at its rim, while in *S.*

saportanus the sepals are continuous with the hypanthium, with no clear attachment point, appearing more as calyx lobes than as individual sepals. The most striking difference between the two species is, however, on the petals: in *S. saportanus* they are concave, coriaceous and are opposite to the sepals/calyx lobes while in *S. pusillus* they are cucullate, thin, and alternate with the sepals. This difference is not evident from the type specimens because those of *S. pusillus* do not have petals preserved. In that case, the sepal morphology can be used to distinguish both species; triangular with a keel in *S. pusillus* and acute with no keel in *S. saportanus*.

At this point, there are not enough characters to assign to assess the identity of *S. saportanus*, however, it is clear that it is not in the genus *Solanites* as this fossil does not fit the definition of the genus. *S. pusillus* on the other hand, is relatively abundant in the flower collections from the Claiborne Formation, allowing for a better assessment of its identity.

***Affinities of* S. pusillus**— The combination of characters present in this taxon: small pentamerous flowers with cupulate hypanthium ending in a thick presumably nectariferous rim, triangular sepals with a prominent midvein or keel, thin clawed cucullate petals alternating with the sepals, and stamens opposite to the petals is not found in the Solanaceae or even in the Asteridae, but in the Rhamnaceae, a family that is today classified with the Order Rosales in the Rosid clade (APG, 1998, 2003). The gross morphology of genera such as *Colubrina*, *Scutia* or *Ziziphus* (Figure 3.4, G-I) is very similar to that of *S. pusillus*. The pollen morphology of the fossil is also consistent with Rhamnaceae: tricolporate pollen with rugulate to striate-rugulate exine is present in *Ziziphus* (Nasri-Ayachi and Nabli, 1995), *Paliurus* (Schirarend, 1996),

Hovenia (Zhang and Chen, 1992), and *Sageretia* (Perveen and Qaiser, 2005); but not in *Rhamnus*, *Frungula* (Punt et al., 2003), or *Colubrina* (Zhang and Chen, 1992).

The phylogenetic analysis conducted in this study yielded two trees, one with *S. pusillus* as sister to *Condalia* and as sister to *Krugiodendron* in the other, well nested in Tribe Rhamneae (Figure 3.10). However *S. pusillus* has a few characters that a distinguishes it from its putative closer relatives, for example its pubescence, a character not present in *Krugiodendron* or in *Condalia* (Medan and Schirarend, 2004). Pubescence is not a common feature among Rhamnaceae but it can be found in other genera such as *Adolphia*, *Discaria*, *Kentrorhamnus*, *Retanilla*, or *Trevoa* (Medan and Aagesen, 1995). Only with more detailed studies, the position of *S. pusillus* within the Rhamnaceae can be more confidently established. However, the recognition of *S. pusillus* as a member of the Rhamnaceae is a significant step towards a better understanding of the fossil history of that family. The abundance of specimens of this taxon (Table 3.7), the good degree of preservation and the previous observations made on this taxon (i.e. Crepet 1974, 1979, 1984) allow for a more thorough study of the biology of this taxon, study that will be presented in a separate paper. Suffice to say that *S. pusillus* is a bona fide member of the Rhamnaceae and therefore not a member of the Solanaceae as was originally suggested (Berry, 1930).

Cantisolanum daturoides— The observation of the only specimen known of this taxon reveals that the fossil is fragmentary and does not have good structural data preserved. In addition, by comparing the original photographs with the fossil in its current state, it can be concluded that a significant amount of pyrite decay has occurred since its original description. The dissection of the fossil and the decay could have obscured or eliminated some features that the original authors observed in the

fossil but that today are not evident. For example, the three abortive seeds mentioned in the protologue (Reid and Chandler, 1933) are nowhere to be found today. The lack of diagnostic characters precludes the assignment of this fossil to the Solanaceae or any other higher taxon (Collinson, 1983).

CONCLUSION

Of all the fossil species studied, only *S. brongniartii* and *S. crassus* might have solanalean affinities, however not with the Solanaceae but with other families of the Order Solanales. After careful revision of the types and in some cases additional specimens of fossil taxa once described as Solanaceae, the conclusion to reach is that none of the fossils studied here belong in the Solanaceae. One of the species, *S. pusillus,* was confidently assigned to the Rhamnaceae, and three more –*S. sarachaformis, S. saportana* and *Cantisolanum daturoides*– were shown to have too little characters preserved to confidently assign them to a family. As of today, the fossil history of the Solanaceae remains elusive.

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